The Social System and Reproduction in a New Zealand Magpie Population, and a Test of the Cooperative Breeding Hypothesis.

A Thesis Presented in Partial Fulfilment
of the Requirements for the Degree of
Doctor of Philosophy in Zoology
at Massey University.

Clare Johanna Veltman

1984

Abstract

Magpie social behaviour was studied at Linton in the Manawatu, from June 1978 to November 1982. Social behaviour patterns and reproduction were investigated, and the hypothesis that magpies were cooperative breeders was tested.

There were two population phases. Nomadic flocks formed in spring and foraged on open, treeless pasture. The flock sex ratio was determined from morphometric measurements, and was between 33:66 and 50:50 males to females. Flock density stabilised at 1 magpie per hectare, and the estimated daily survival rate was 0.9. Territorial magpies defended all-purpose areas averaging 5 hectares in size, and there was no correlation between territory size and the number of occupants. The mean adult survival rate was 0.85, and annual productivity was 0.96 juveniles per breeding female.

Flock magpies associated randomly, and flock membership changed frequently. The primary activity of flock birds was foraging, which intensified during the afternoons, and in the month of March. The proportion of flock magpies foraging was positively correlated with the number of birds present.

Territories were defended by pairs and groups. Non-kin groups may have formed in the flock, and kin groups formed when juvenile dispersal was delayed. Non-breeders did not help at the nest, and male parents made as many visits to nestlings as females did. Time of day strongly influenced the distribution of activities, so that foraging occupied more time in the afternoons. Group-territory magpies spent less time perching and more time defending the territory than pair-territory birds.

The average national clutch size was 3.5 eggs. There was no difference in the breeding output of pair-territory and group-territory hens, but *per capita* production was lower in the groups. Average individual fitness estimates were prepared for each of four magpie lifestyles, and were highest for pair-territory birds.

Supplementary food did not inhibit juvenile dispersal, and lead to polygyny in the formerly pair-defended territories. Hens receiving extra food fledged more juveniles than they had in the previous spring.

It was argued that magpies were not cooperative breeders, but selfish opportunists which exploited various social lifestyles in order to obtain reproductive status.

ACKNOWLEDGEMENTS

The advice and help received from many people during the study is gratefully acknowledged.

Messers Harrington, Greatorex, Manning, Crowley, Underwood, McGovern and Irvine, and the managers of the Kilsby Estate all granted permission for their properties to be freely entered.

Jane Hughes (Griffith University, Brisbane) and Wim Vestjens (late of C.S.I.R.O., Canberra) discussed magpie trap designs and problems, and Neil Murray (La Trobe University, Melbourne) described his method for scoring magpie plumages.

Bob Kreymborg helped with the construction of traps and cages, and made the pole-mounted mirror used to examine nests.

David Crockett made available the nest record cards collected by members of the Ornithological Society of New Zealand Inc. for analysis, on behalf of the Society.

Christine Reed cut and delivered about half of the meat consumed during the food-addition experiment, while employed as a temporary technician in the Botany and Zoology Department.

Walt Abell and Robert Lambourne of the Massey Computer Centre

taught the author to compile SPSS and Genstat programmes, and Robert Lambourne and Greg Arnold (Department of Mathematics and Statistics) helped to unravel problems with analyses of variance.

John Craig (University of Auckland) critically appraised drafts of Chapters Two to Six inclusive, and offered helpful advice on presentation.

Neil Pinder drew Figures 3.a, 3.b, 4.j, 4.k, and 4.1, arranged the photocopying, and assisted in many other ways with the production of the thesis.

This project was supervised by Prof. Brian Springett who helped with some of the field work, and read and commented on each of the chapter drafts.

Robert Carrick and Lou Gurr provided solid encouragement, stimulating conversation and generous hospitality throughout the study. Their ideas challenged the author and helped to shape the thesis.

To them, and all those listed above, sincere thanks.

CONTENTS LIST

Page

ABSTRACT ii

ACKNOWLEDGEMENTS iv

CONTENTS vii

LIST OF TABLES xiii

LIST OF FIGURES xv

LIST OF PLATES xvii

CONTENTS LIST

Page

CHAPTER ONE 1

Introduction

1.0.0 The Evolutionary Paradigm 1

1.0.1 Aim of the Study 2

1.1.0 Taxonomy of the Gymnorhinae 3

1.2.0 Habitat, diet, predators and pathogens of magpies 4

1.3.0 Introduction to New Zealand 4

1.4.0 Magpie longevity 5

1.5.0 Contents 6

- 1.5.1 Contents of Chapter Two 6
- 1.5.2 Contents of Chapter Three 6
- 1.5.3 Contents of Chapter Four 6
- 1.5.4 Contents of Chapter Five 7
- 1.5.5 Contents of Chapter Six 7
- 1.5.6 Contents of Chapter Seven 8

CHAPTER TWO 9

Dispersion and Spacing Mechanisms in the Linton Population

2.0.0 Introduction 9

2.1.0 Methods 11

Page

2.1.1 Study area 11

2.1.2 Live trapping 12

2.1.3 Morphometric measurements 12

2.1.4 Banding 14

2.1.5 Sex and Age classes 14

2.1.6 Colour classes 15

2.1.7 Exploratory observations 15

2.1.8 Sampling density 20

2.1.9 Statistical Analyses of morphometric measurements 22

2.1.10 Calculation of dispersion measure 23

2.2.0 Results 24

2.2.1 Two population phases 24

2.2.2 The nomadic flock 25

2.2.3 Magpie territories 33

2.2.4 Magpie dispersion in the study area 40

2.2.5 Stereotyped display behaviour 42

2.2.6 Singing behaviour 44

2.3.0 Discussion 45

CHAPTER THREE 51

Flock Cohesion and Behaviour

3.0.0 Introduction 51

3.1.0 Methods 53

Page

3.1.1 Trapping and Banding 53

3.1.2 Sampling behaviour 53

3.1.3 Behaviour Patterns 54

3.2.0 Results 56

3.2.1 Associations between magpies 56

3.2.2 Time-activity Distributions 56

3.3.0 Discussion 64

CHAPTER FOUR 70

Territory histories and time-activity distributions

4.0.0 Introduction 70

4.1.0 Methods 76

4.1.1 Trapping and Banding 76

4.1.2 Sampling behaviour 76

4.1.3 Behaviour classes 78

4.1.4 Statistical Analyses of Time-Activity scores 80

4.2.0 Results 81

4.2.1 Number and distribution of territories 81

4.2.2 Annual cycle of activity 81

4.2.3 Inter-territory behavioural interactions 82

4.2.4 Defense by pairs and groups 87

Page

4.2.5 Composition of groups 87

4.2.6 Intra-territory relationships 88

4.2.7 Sexual behaviour 91

4.2.8 Cooperative breeding 93

4.2.9 Juvenile and sub-adult dispersal 94

4.2.10 Time-activity distributions 95

4.3.0 Discussion 116

CHAPTER FIVE 130

Reproduction in the Linton population

5.0.0 Introduction 130

5.1.0 Methods 133

5.1.1 Searching for nests 133

5.1.2 Examination of nest contents 134

5.1.3 Monitoring breeding progress 134

5.1.4 Annual census 134

5.2.0 Results 134

5.2.1 Clutch sizes 134

5.2.2 Nestling and fledgling survival 136

5.2.3 Reproduction in pair- and group-defended territories 137

5.3.0 Discussion 141

Page

CHAPTER SIX 151

Food Addition Experiment

6.0.0 Introduction 151

6.1.0 Methods 152

6.1.1 Test and Control territories 152

6.1.2 Description of food stations 153

6.1.3 Description of supplementary food 153

6.1.4 Experimental regime 153

6.1.5 Sex of dispersing juveniles 155

6.2.0 Results 155

6.2.1 Juvenile dispersal 156

6.2.2 Polygyny in test territories 156

6.2.3 Productivity in test and control territories 159

6.3.0 Discussion 161

CHAPTER SEVEN 167

Discussion and Summary

7.0.0 Discussion 167

7.1.0 Parameters of a magpie population in New Zealand 167

7.1.1 Population size and density 168

Page

7.1.2 Clutch size and productivity 168

7.1.3 Survival 170

7.1.4 Operational sex ratios 170

7.2.0 Four lifestyles in a New Zealand magpie population 170

7.2.1 Nomadism versus territoriality 171

7.2.2 Monogamy versus group-territoriality 173

7.3.0 The cooperative breeding hypothesis 173

7.3.1 Strong inference 174

7.3.2 Cooperative breeding 175

7.3.3 Delayed juvenile dispersal 175

7.4.0 Summary 178

APPENDIX 180

REFERENCES 182

LIST OF TABLES

Table		Page
2.a	Magpie age classes.	16
2.b	Morphometric measurements of flock magpies.	27
2.c	Results of discriminant function analysis on tarsus, toe and beak length measurements of 18 sexed magpies and 33 unsexed magpies.	29
2.d	Population parameters estimated from flock recaptures, using Fisher-Ford method.	31
2.e	Morphometric measurements of territorial males and females.	36
2.f	Morphometric measurements of Age Class 3 magpies.	37
2.g	Summer census counts of territorial magpies.	39
2.h	Summer census counts of 12 closely-watched territories.	39
3.a	Distribution of possible-pair sightings.	57
3.b	Flock time budget sampling effort.	58
3.c	Analysis of variance on number of flock birds per scan, by month and time, excluding September.	60
3.d	Analysis of variance on transformed proportions of flock magpies foraging, by month and time, excluding September.	62
3.e	Regression analysis of flock size and foraging activity.	63
4.a	Group composition at January 1980 census.	89
4.b	Summary of sampling effort for territory time budgets in real-time minutes.	97
4.c	Hypotheses.	101
4.d	Analysis of variance on time spent foraging by month and time, for territory magpies.	103
4.e	Analysis of variance on time spent perching by month and time, for territorial magpies.	105
4.f	Analysis of variance on time spent defending the territory, by month and time.	108

Table Page

4.g Time budget and territory size changes predicted by Schoener's (1983) model of energy-maximising territory holders with processing constraints. 125

5.a Nestling number counted from clutches of known size. 138

5.b Production of juveniles by breeding female magpies. 139

5.c Fledgling success estimated from clutch sizes of 3.5. 140

5.d Female productivity in pair- and group-defended territories. 142

5.e Production *per capita* by adults in pair- and group-defended territories. 143

5.f Number of juvenile magpies fledged in groups of various sizes. 144

5.g Estimated average individual fitness. 149

6.a Length of stay by juvenile magpies (estimated) during food-addition experiment. 157

6.b Number of yearling magpies remaining and nests built in test and control territories at completion of food-addition experiment. 158

6.c Number of juveniles fledged by female magpies in test and control territories. 160

6.d Number of juveniles fledged per breeding female in 1981 and 1982, for test and control territories. 162

APPENDIX

1 Number of visits and sights in 12 closely-watched magpie territories, and number of sightings needed for 90% census efficiency (when visit efficiency of 60% is set). 180

LIST OF FIGURES

Figure Page

2.a Back plumage patterns ranging from white-backed (A) to black-backed (E) magpies. 18

2.b Distribution of flock magpies in the Linton study area, and location of a short-term territory established by flock birds. 26

2.c Approximate boundaries of thirty numbered magpie territories in the Linton study area, with dates of first observations. 34

2.d Stereotyped display behaviour of magpies. 43

3.a Variation in flock sizes measured during six day-time periods for twelve months. 61

3.b The percentage of flock magpies performing each activity during six day-time periods for twelve months. 65

4.a The distribution of territory defence activity in each day-time period for four seasons. 84

4.b Movements of four magpies banded in territory [09], August 1978. 86

4.c Pre-mating display by female magpies. 92

4.d Percent time expended in three predominant activities from November to July by territorial magpies. 98

4.e Male and female magpie time budgets in the breeding season. 99

4.f Seasonal patterns of foraging activity by territorial magpies, over six day-time periods. 104

4.g Seasonal patterns of perching activity by territorial magpies, over six day-time periods. 107

4.h (1) Individual foraging scores. 109

4.h (2) Individual foraging scores continued. 110

4.h (3) Individual foraging scores continued. 111

Figure		Page
4.i	(1) Individual perching scores.	112
4.i	(2) Individual perching scores continued.	113
4.i	(3) Individual perching scores continued.	114
4.j	Distribution of anti-predator behaviour by pair- and group-territory magpies.	117
4.k	Distribution of social interactions of pair- and group-territory magpies.	118
4.l	Distribution of play behaviour by pair- and group-territory magpies.	119

APPENDIX

1	Sightings of individually banded flock magpies from October 1978 to April 1979.	181

LIST OF PLATES

Plate		Page
2.a	Territory trap, containing decoy bird. Two magpies sing in response to the decoy stimulus, and two other magpies exhibit the bill-down display.	13
2.b	Flock trap.	13
2.c	Fledgling magpie.	17
2.d	Adult male magpie.	17
3.a	Flock magpies perching, preening and foraging.	67
4.a	Male magpie provisions three nestlings.	120
5.a	Pole-mounted mirror used to view magpie nest contents.	135
6.a	Feeding station.	154
6.b	Male magpie consumes ox-heart at feeding station.	154

CHAPTER ONE

Introduction

1.0.0 The evolutionary paradigm.

Adaptations are attributes which permit organisms to 'accomplish those immediate objectives' which must be achieved in order to survive and reproduce successfully (Dunbar 1982), and vary between individuals. Since some of the individual variation is inherited, the outcome of interactions between organisms and their environments may be measured as the rate of spread of the attributes in the gene pool, or fitness. Natural selection is the process through which environmental pressures on individuals effect changes in gene frequency, establishing adaptations in the gene pool.

The role of natural selection as an optimizing agent was queried by Gould and Lewontin (1979), who criticized biologists for reducing organisms to collections of unitary traits and then proposing a separate adaptive explanation for each. By defining adaptations as the result of natural selection, and then defining natural selection as the process leading to the acquisition of adaptations, such biologists were said to be reducing the theory of natural selection to a tautology. Since then, several theoretical treatments have demonstrated that no tautology exists when natural selection theory is rigorously stated (Reed 1981, Dunbar 1982, van der

Steen 1983).

However the empirical demonstration of natural selection remains problematic. Mayr (1983) recently argued that adaptationist hypotheses are valid since they must be systematically tested and excluded before the operation of chance can be invoked. The evolutionary paradigm described and defended by Mayr provided the practical framework for this study. Because selection acts on individuals, magpie sociality was examined from the standpoint of individual magpies. The range of social responses made by magpies was investigated, and their reproductive output was measured in relation to lifestyle. In this way, it was possible to evaluate the "adaptiveness" of magpie social patterns. Apparently non-adaptive altruistic acts (those that increase the individual fitness of another animal while reducing the individual fitness of the actor) which contradicted natural selection theory were then investigated more closely.

1.0.1 Aim of the study.

An investigation of magpie social behaviour was initiated in mid-1978, in order to discover how magpies in New Zealand responded to intraspecific competition for food and space, and to test the hypothesis that some magpies bred cooperatively.

Since variation is the raw material of natural selection, inter-individual differences in social behaviour were examined and their reproductive consequences measured. A demonstration that individuals within social units compete for reproductive opportunities would allow the effect of natural selection on the various lifestyles to be evaluated.

1.1.0 Taxonomy of the Gymnorhinae.

Gymnorhina is one of three genera in the Australo-Papuan avian family Cracticidae, and refers to the Australian magpies. Three geographically distinct types of magpie occur in Australia, but since they interbreed freely in the areas of overlapping range a common binomial, *Gymnorhina tibicen*, is used (Schodde 1975, Dow 1980, Pizzey 1980, 1983). This replaced the former trinomials (*Gymnorhina t. tibicen* for the northern black-backed form, *Gymnorhina t. hypoleuca* for the southern white-backed form), and the separate species status of the Western form, *Gymnorhina dorsalis* (Serventy 1969). A genetic mechanism for the variation in back plumage colours between white- and black-backed magpies was proposed by Hughes (1982).

At present, magpies in New Zealand are classed into subspecies (O.Soc.N.Z. 1970), presumably because they are geographically isolated from the native populations (see a discussion of subspecies by Phillips 1982, Zusi 1982, Parkes 1982). However, phenotypic uniformity of white- and black-backed magpies in New Zealand is lacking, and a range of plumage patterns may be seen. For this reason it was impossible to accurately identify the magpies in the study population to subspecies level. The population comprised white- and black-backed forms of the Australian magpie, *Gymnorhina tibicen*.

1.2.0 Habitat, diet, predators and pathogens of magpies.

In the Australian environment, magpies occupy open savannah woodlands and farmed pastures (Carrick 1972), and are nonmigratory. They eat "a wide range of ground arthropods, mainly insects and spiders, and also earthworms" (Vestjens and Carrick 1974).

The Australian raven (*Corvus coronoides*) preys on eggs and young nestlings, and adults are taken by foxes and feral cats (Carrick 1972), as well as by humans.

Magpies are infected by a variety of pathogens. Deaths due to *Staphylococcus*, *Pasteurella* and *Aspergillus* infections were reported by Carrick (1972), and Harrigan and Arundel (1978) described *Syngamous trachea* in a white-backed magpie. White-backed magpies have also been reported with poxvirus infections (Harrigan *et al* 1975).

1.3.0 Introduction to New Zealand.

McIlroy (1968) has summarised the available information on the introduction of magpies to New Zealand, based on the report by

Thomson (1922) and subsequent notes in the literature.

The first birds were probably those from Victoria liberated in Canterbury between 1864 and 1867, to control insect pests of pasture. Many introductions followed throughout New Zealand during the next thirty years, and now magpies are distributed throughout the low-altitude areas of both main islands (Bull _et al_ 1978).

1.4.0 Magpie longevity.

Magpies are long-lived birds with age-spans of up to eighteen years in the wild (Carrick 1972), and in captivity (McCaskill 1945). Evolutionary studies of social strategies require lifetime reproductive data from individuals (Vehrencamp 1979), presenting the students of potentially cooperative subtropical species (Emlen 1978) with severe logistical problems (Balda 1981).

There is an alternative approach which circumvents the necessity for such long-term investment of effort, at least in part. Called strong inference (Platt 1964), it is the classical approach to scientific research. A series of falsifiable hypotheses are systematically tested until one hypothesis is found which cannot be disproved by experimental results. Strong inference allowed cooperative breeding in magpies to be investigated in a relatively short time span.

1.5.0 Contents

Each chapter following was designed to be self-sufficient, so that the methods and discusion appropriate to the data were in immediate proximity.

1.5.1 Contents of Chapter Two.

A description of the study area and the distribution of magpies in that area is supplied in Chapter Two. The size of the population was estimated, and different patterns of resource use and site-attachment studied. Survival, migration and reproduction were investigated, and comparisons were drawn with an Australian population.

1.5.2 Contents of Chapter Three.

In Chapter Three, the cohesiveness and everyday behaviour of nomadic magpies living in a flock are described. From resightings of banded birds it was possible to compare the pattern of individual associations with a pattern that would be expected if flock magpies arrived and departed randomly from the flock area. A study of time budgets allowed the behaviour patterns of flock magpies to be catalogued, and foraging behaviour to be studied.

1.5.3 Contents of Chapter Four.

Behavioural interactions within and across territory boundaries are summarised in Chapter Four. Changes in the composition of social groups were monitored, and led to an understanding of group origins. A time budget study allowed behavioural differences between individuals to be linked to reproductive and social status.

1.5.4 Contents of Chapter Five.

The breeding performance of female magpies in different social units was compared, in order to discover whether productivity was enhanced by the proximity of nonbreeding companions or offspring. If female magpies living in group-defended territories reared more offspring than their counterparts in smaller social units, then the hypothesis that magpies were cooperative breeders could be accepted. These and annual production data for four breeding seasons are presented in Chapter Five.

1.5.5 Contents of Chapter Six.

The results of a food-addition experiment which tested the hypothesis that juvenile magpies emigrate from their natal territories in response to a food shortage are given in Chapter Six. A characteristic of cooperatively breeding species is the delayed dispersal of offspring, and this research aimed to discover why delayed dispersal occured so infrequently in the study population.

1.5.6 Contents of Chapter Seven.

Chapter Seven contains a formal defence of the thesis that magpies in the Linton population did not breed cooperatively, and that their social responses were selfish rather than altruistic. It is argued that magpies exploited a range of lifestyles in the transition to reproductive status.

CHAPTER TWO

Dispersion and Spacing Mechanisms in the Linton Population

2.0.0 Introduction

Animal social systems evolve in response to environmental pressures on life-history features (Gadgil and Bossert 1970, Dunbar 1983). To understand a social system, it is therefore necessary to know the demographic regime of the species in question (Fitzpatrick and Woolfenden 1981). The objective of this chapter is to describe the demographic processes of spacing and resultant dispersion in a New Zealand population of magpies, and to compare these features with those recorded in an Australian population (Carrick 1963,1972).

The first question to be posed was, how were magpies dispersed in the New Zealand population? Dispersion commonly refers to the distribution of animals in space at one moment in time, and in many species the pattern of dispersion reflects the association of individuals in primary social units - the smallest social unit in which members can survive and reproduce normally (Brown and Orians 1970). More than one type of social unit has been previously described in a magpie population (Carrick 1963, and see section 5.0.0), and this investigation aimed to establish whether similar complexity occurred in a New Zealand population. First, magpies in the study area were banded, mapped and counted in order to discover both nomadic and sedentary birds. Then, since dispersion is density-dependent (Taylor et al 1978), the density and spatial distribution of the sedentary birds was found in order to anticipate trends in population dynamics.

The nomadic phase of the population was then examined more closely. What age and sex were the nomadic individuals? The measurements of trapped birds of known sex were used to create a discriminant function for sexing unknown magpies, and a comparison of the sizes of mature and immature birds was made. How many magpies were nomadic, and when did they leave the sedentary phase? Capture-recapture analyses of banded birds were performed to estimate the number of nomadic birds, and the formation of nomadic flocks was monitored during regular field inspections.

Focus then shifted to the sedentary magpies. How many birds in the study area defended territories, what was their density, and did their numbers vary from year to year? Linked to this was the question of territory occupancy; was territory size correlated with the number of magpies living within the boundaries? These questions were answered from census data and the average annual productivity was also calculated from these data.

Finally, the behavioural mechanisms which allowed magpies to space themselves with respect to each other were examined. Song and stereotyped postures served as devices to manipulate the behaviour of conspecifics (in the sense of Hinde 1981), and attempts to describe these elements were made.

Even within the reproductive phase of an animal population, asymmetries in sex, reproductive value, experience, dominance and kinship lead individuals to adopt different behavioural strategies from each other (Emlen 1981). In this chapter the demographic stage is set for a study of individual differences in lifestyle and reproductive performance.

2.1.0 Methods

2.1.1 Study Area

Fieldwork was concentrated in the area bound by Hewitt's Road, State Highway 57, Kendall's Line and the foothills of the Tararua Mountain Range at Linton in the Manawatu region. Linton is 175^{o}36'E in longitude and 40^{o}26'S in latitude.

The 3.03 km^{2} area constituted five farms; three dairy units, one dry-stock run, and one sheep and beef unit. Ryegrass and ryegrass/clover pastures were maintained on a clay-loam soil. Apart from one small copse of native tree species in the study area, the irregularly occurring shelterbelts were dominated by pine (*Pinus radiata*) and macrocarpa (*Cupressus macrocarpa*) trees.

The Manawatu district is characterized by an average annual rainfall of 986 mm^2, and prevailing westerly winds. Monthly mean temperatures (from data collected at D.S.I.R. Palmerston North over thirty years) range from 8.2°C in July to 18.1°C in February.

2.1.2 Live Trapping

Sub-adult and adult magpies were trapped in the study area for banding from June 1978 to May 1980. The trapping technique was developed from a method described by J. Hughes (pers. comm.). A wire-netting trap measuring 1.3m x0.90m x0.90m was erected at the centre of a territory and fitted with four funnel entrances at ground level. One live decoy magpie was placed inside the trap in a smaller cage. Rolled oats were scattered on the ground near the entrances. This device is illustrated in Plate 2.a.

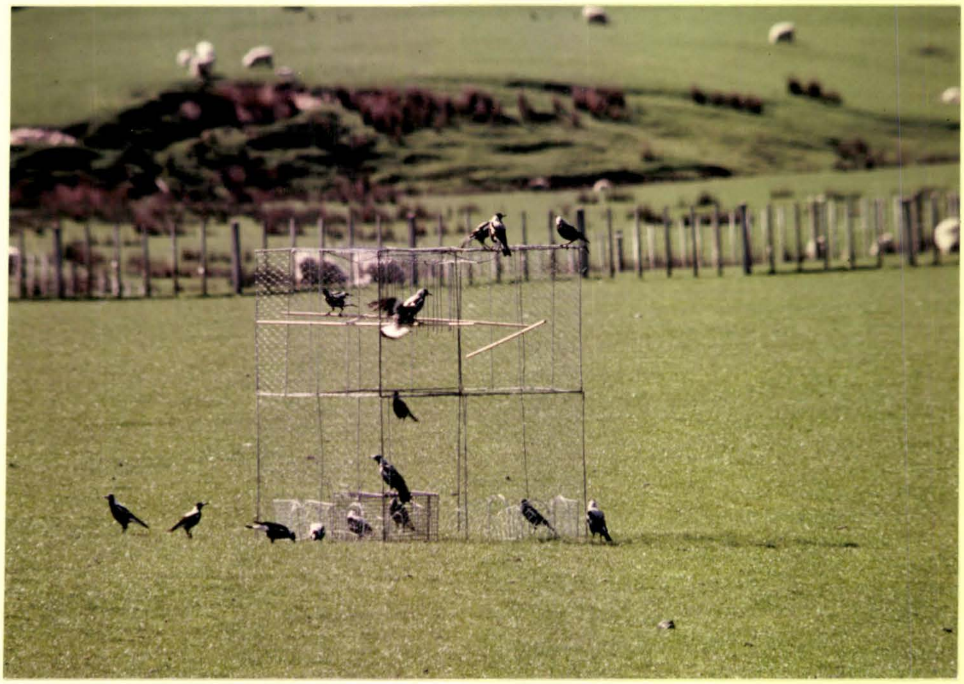
Flock birds were trapped in the same manner but in a larger wire-netting trap measuring 1.8m x1.8m x1.8m. Up to twenty magpies were collected at once by this method. See Plate 2.b.

Once caught in the trap, magpies were captured by hand and transferred to calico bags fitted with ventilation holes and draw- string tops.

2.1.3 Morphometric Measurements

PLATE 2.a. Territory trap, containing decoy bird. Two magpies sing in response to the decoy stimulus, and two other magpies exhibit the bill-down display.

PLATE 2.b. Flock trap.



Captured magpies were measured as follows. Weight to the nearest gram was read from a spring balance (Salter), and corrected for bag-weight; bill length, width, and depth were measured with Vernier calipers; tarsus, toe, and toenail lengths were found by extending dividers to the limits of the limbs and reading the lengths from a metal ruler; wing and tail lengths were measured directly by the same metal ruler. All measurements were entered onto individual record cards.

The statistical analyses of these data are described in section 2.1.9.

2.1.4 Banding

A total of 62 magpies were banded in the Linton study area between June 1978 and May 1980. The left leg received one stainless steel numbered and one coloured plastic band, while the right leg was fitted with a unique combination of three coloured plastic bands.

2.1.5 Sex and Age Classes

Sexes were determined with reference to plumage criteria. Adult male magpies exhibited 'shining' white nape and back feathers, while the same feathers on females were grey. Males were also slightly larger than females (see 2.2.4) but this characteristic was not useful for the visual sexing of birds in the field.

Six age classes were recognised, based on physical appearance. They are summarised on Table 2.a. Difficulty was experienced in visually separating adult females (Age Class 6) from subadults of either sex (Age Class 5). In practice,identification of an animal as an adult female was certain only in territories defended by a monogamous pair, and had to be confirmed for other magpies by observation of female-like reproductive activity.

2.1.6 Colour Classes

An arbitrary classification of the variations in back plumage colour was developed, after a similar system by N. Murray (pers. comm.). Birds handled during trapping were assigned a colour class, as were all magpies whose behaviour was noted during the project. The range of variation in back plumage is illustrated in Figure 2.a.

A photographic plate illustrating the variety of back plumage in the black-backed magpie was published by Cole (1921).

2.1.7 Exploratory Observations

Magpies were located at dawn by tracing the source of bouts of singing. Singing birds were then monitored until they flew to the ground to commence foraging. Those animals flying less than 300m. to their foraging positions were tentatively

TABLE 2.a

Magpie age classes

Class	Stage of Development
1	nestling
2	fledgling. *See Plate 2.c.*
3	less than one year in age
4	less than two years in age.
5	subadult, less than four years
6	adult. *See Plate 2.d.*

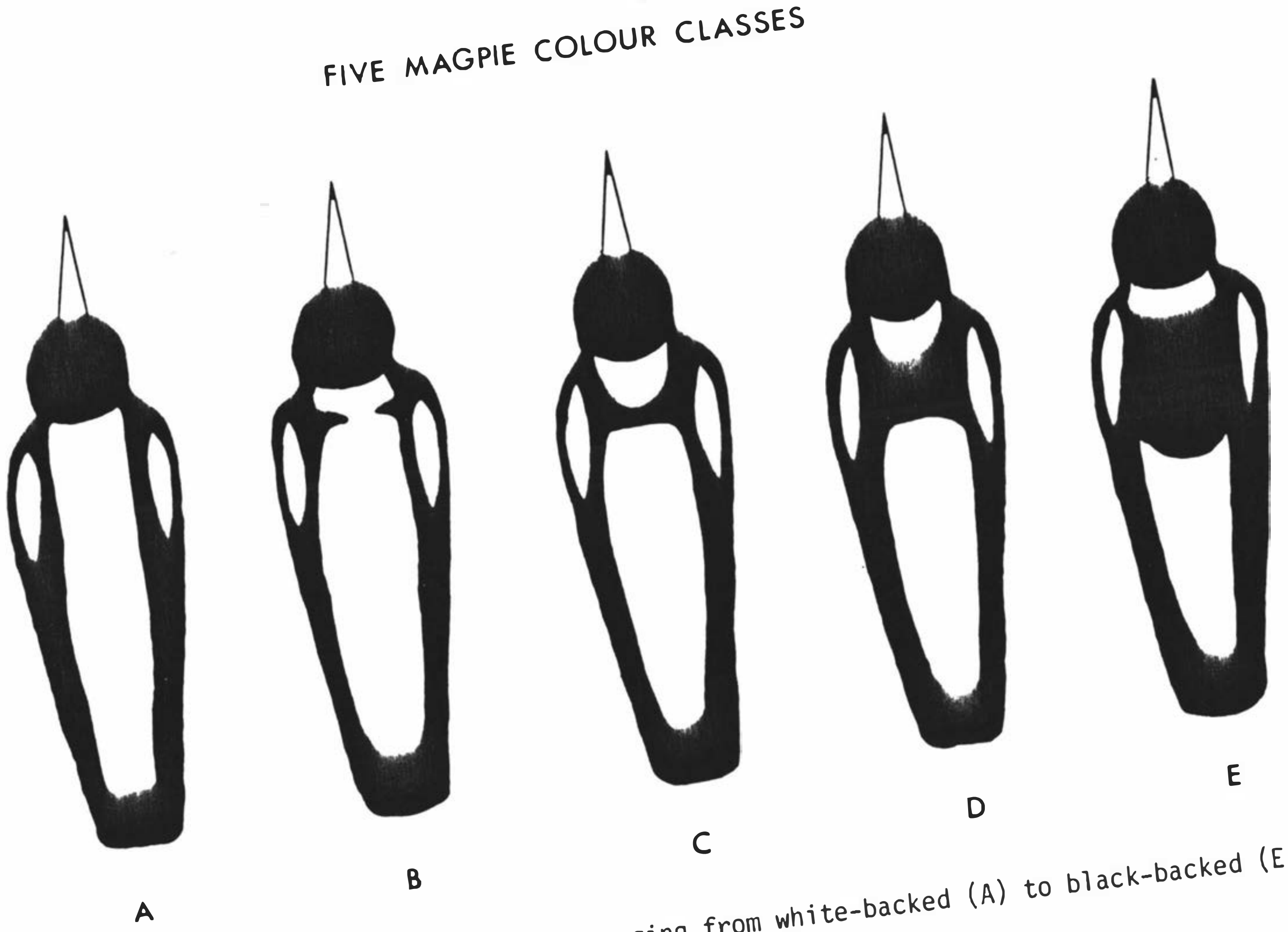


FIGURE 2.a. Back plumage patterns ranging from white-backed (A) to black-backed (E) magpies.

considered to be territorial in that area. Territoriality was confirmed by attendance at a nest in the vicinity, or through the observation of aggressive interactions with nearby magpies. Once identified, territories were named with reference to a prominent geographic feature. (Following Davies (1978), territories were recognised whenever the birds were spaced out more than would be expected from random occupation of the habitat).

The study area was traversed on foot at intervals, and the presence or absence of individuals was noted. The results of each circuit were entered onto territory or flock logs, so that a history of each magpie locality was compiled.

Behavioural observations of both banded and unmarked magpies were conducted from portable nylon hides (manufactured at Len Shailer Ltd., Palmerston North) erected near the birds, or from positions of concealment in nearby clumps of vegetation. Average flight distances (the distance between observer and subjects when the subjects take flight) were too great to allow opportunistic observations to be made.

A 'no-restraint' or ad libitum method of sampling behaviour was employed (Altmann 1974). Ad libitum observations were made with the aid of 10 x 40 binoculars (Zeiss) and recorded into field notebooks. Resultant data were descriptive in form so that assumptions about the true probability of observing individuals and behaviour patterns did not have to be satisfied (Altmann 1974,Lehner 1979). This sampling technique provided a formal format for the early exploration of the study area, without excluding fortuitous observations of unusual or rare events.

2.1.8 Sampling Density

To obtain estimates of population density, the number of magpies living within the boundaries of the studied area was found (population size), and expressed in relation to the measured size of the study area.

The size of the study area was found from a composite aerial photograph which had been calibrated from 8 measurements of real distances between landmarks. Territory sizes were found by tracing approximate territory boundaries onto transparent draughting paper, and weighing the pieces of paper encompassed by each perimeter. The weight of a $10mm^2$ piece of the same paper was employed to determine the territory sizes represented by each measurement. A Mettler AE160 balance was used. Boundaries were only approximate because magpies were not observed to defend all limits of their territories, and because the outlines were not drawn from marks made in the field.

Separate population density estimates were prepared for locally distributed mobile magpies and sedentary magpies. A capture-recapture technique developed by Fisher and Ford

(1947) for several releases and several recaptures (Begon 1979) was applied to the data collected from mobile birds. Population size was estimated by assuming that the ratio of marks to total individuals in a day i sample is the same as in the total population:

$$N_i = \frac{(n_i+1).M_i}{(m_i+1)}$$

where N_i =estimated population size on day i

n_i =the number of individuals caught on day i

m_i =the number of marked individuals caught on day i

M_i =the number of marks at risk on day i.

M_i was calculated by comparing the days survived by marks in the samples with the days survived by marks in the population. Initial captures were banding events and later 'recaptures' were made during routine watches of the nomadic flock.The Fisher-Ford method assumes that survival rate is constant, and in common with other capture-recapture methods demands that marks are permanent (and correctly identified);that individuals are unaffected by marking; that all individuals have an equal chance of being caught; and that all individuals have an equal chance of dying or emigrating (Begon 1979). The estimated parameters are derived by grouping data together to produce a single survival-rate. Samples are combined and sampling errors therefore tend to cancel out.

Sedentary birds were sampled by the area count or spot-map method (Davis 1982), despite the interpretational problems inherent in the technique (Best 1975). The study area was systematically searched and magpies seen or heard were noted. This procedure allowed direct enumeration of sedentary birds, and a map of bird locations was developed.

The efficiency of censusing by the territory mapping technique was estimated using the method published by Svensson (1978). It was shown from a binomial model that as visit efficiency (the ratio between the result of a single visit and the true number of territories) increased to 80%, then 99% of the territories should be identified after 5 valid visits with an acceptance level (minimum number of point-records required) of 2. From the published table it was then possible to determine the minimum number of registrations required for various numbers of valid visits, in order to obtain 90% census efficiency from visits of 85% efficiency.

2.1.9 Statistical Analyses of Morphometric Measurements.

Twosample t-tests of the differences between variable means for each age class were conducted (without assuming equal variance) using MINITAB (Ryan,Joiner and Ryan 1976).

The measurements on seven variables (weight, tarsus length, toe length, toenail length, beak length, beak depth, and beak width) obtained from the trapped sample of adult magpies of known sex were subjected to a discriminant function analysis. This technique permitted an optimal linear combination of the variables to be developed, for use in sexing other trapped magpies on the basis of morphological measurements alone.

The basic strategy in discriminant function analysis is to form a linear combination of the measured variables similar to

$$L=B_1X_1+B_2X_2+....B_pX_p$$

where X_1=variable one

X_2=variable two

X_p=the pth variable

B=a constant

and there are n_1 individuals in group (population) 1, and n_2 individuals in group (population) 2 (Kleinbaum and Kupper 1978).

A dummy variable indicating group membership (in this case, sex) was created and birds identified as males were scored 1, while females were scored as 2. Magpies of unknown sex were scored 0 and classified as male or female on the basis of L obtained from each individual, after the discriminant function had been calculated from a stepwise regression procedure.

Subprogramme DISCRIMINANT in the SPSS series was employed for this analysis (Nie, N.H. et al 1975).

2.1.10 Calculation of Dispersion Measure.

A quantitative measure of spatial relationships in populations is the distance to nearest neighbour, developed by Clark and

Evans (1954). The nearest neighbour analysis is a measure of the manner and degree to which the distribution of individuals in a population on a given area departs from that of a random distribution (Clark and Evans 1954). The ratio of the mean of measured nearest neighbour distances to the mean distance which would be expected if the population were randomly distributed is calculated, and used as a measure of the degree to which the observed distribution approaches or departs from random expectation. In a random distribution R=1, under conditions of maximum aggregation R=0, and under conditions of maximum spacing R=2.1491. If R indicates that the population is not randomly distributed, then the significance of the difference between means can be determined from the Pearson type III distribution.

In this study, each 'neighbour' was the nexus of a territory. The territory nexus corresponded to that place in the territory which was observed to be most favoured by the occupants, and was usually also the location of nest sites.

2.2.0 Results

2.2.1 Two Population Phases.

Two population phases were distinguished on the basis of use-of-space criteria.

1528 sightings of site-attached (sedentary) magpies were logged between June 1978 and May 1982. These birds were found to be actively defending areas pivoted about tree clumps or lengths of treeline.

Almost 400 sightings of nomadic birds were logged during the same period. These animals foraged in flocks on undefended pastures in the study area, and were observed to roost together in tree-clumps at the edge of the area. An unknown number of magpies fed within the study area, but made long, high dawn and dusk flights to other destinations.

2.2.2 The Nomadic Flock.

A flock of 35 magpies was first observed in the study area on 28-8-78. A week later 44 birds were counted at the same locality, shown on Figure 2.b, and regular periods of observation of these birds commenced.

Four separate banding efforts were made in flock grounds between September 1978 and February 1979. A total of 33 individuals were measured and colour-banded; 26 from Age Class Four, 3 from Age Class Five, and 4 from Age Class Six. One-quarter of the trapped sample consisted of partly black-backed magpies (Colour Classes B,C,D), and the remainder were white-backed.

The morphometric measurements are summarised on Table 2.b.

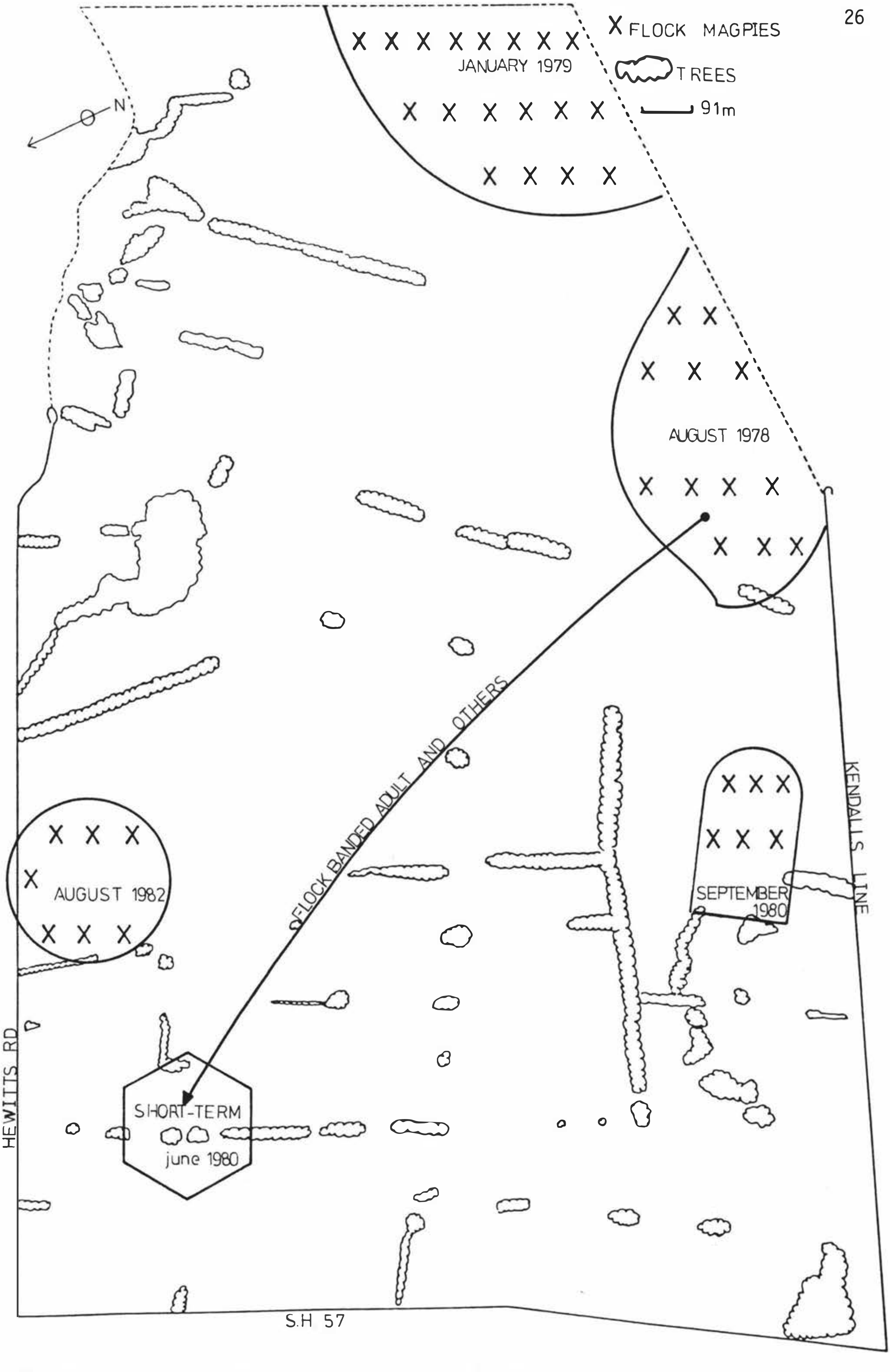


FIGURE 2.b. Distribution of flock magpies in the Linton study area, and location of a short-term territory established by flock birds.

TABLE 2.b

Morphometric measurements of flock magpies

Variable		Age class 4	Age Class 5 + 6	T Test $MU_1 = MU_2$
n		26	7	
Weight (gms)	$\bar{x}$	319.2	345.7	t = -2.85
	S	20.3	22.3	
	$S_{\bar{x}}$	4.0	8.4	P = 0.022*
	max	355.0	380.0	
	min	285.0	325.0	
Tarsus (mm)	$\bar{x}$	55.4	55.4	t = -0.00
	S	3.1	2.8	
	$S_{\bar{x}}$	0.6	1.0	P = 1.0
	max	61.0	60.0	
	min	49.5	52.0	
Toe (mm)	$\bar{x}$	30.5	30.0	t = 0.34
	S	2.3	3.0	
	$S_{\bar{x}}$	0.4	1.1	P = 0.74
	max	36.0	34.0	
	min	26.0	25.0	
Toenail (mm)	$\bar{x}$	11.9	12.2	t = -0.55
	S	0.9	1.2	
	$S_{\bar{x}}$	0.1	0.4	P = 0.60
	max	14.0	14.5	
	min	9.5	10.5	
Beak length (mm)	$\bar{x}$	48.3	52.2	t = -2.11
	S	3.8	4.7	
	$S_{\bar{x}}$	0.7	1.8	P = 0.068
	max	54.0	60.0	
	min	35.5	45.0	
Beak depth (mm)	$\bar{x}$	20.6	21.9	t = -2.00
	S	2.3	1.6	
	$S_{\bar{x}}$	0.4	0.6	P = 0.066
	max	24.0	20.0	
	min	11.0	20.0	
Beak width (mm)	$\bar{x}$	18.1	18.8	t = -0.95
	S	2.4	2.0	
	$S_{\bar{x}}$	0.4	0.7	P = 0.36
	max	21.5	21.0	
	min	10.0	15.0	

where * = $P < 0.05$

Only the bodyweight variable was found to differ significantly between the age classes at the 95% level. Older magpies in the flock were heavier than the younger birds. Beak length and depth measurements tended to be smaller in the younger magpies, but the difference was not significant. Full adult size may not be achieved before 3 years of age.

An attempt was made to classify the flock sample of 33 measured individuals by sex. Nine adult males and nine adult females (see section 2.2.3) formed the data set for a discriminant function analysis. The analysis is summarised on Table 2.c.

The variables tarsus length, toe length and beak length were found (through stepwise regression) to contribute the most useful measures in the discriminant function. When applied to the initial sample of 18 adults of known sex, the function correctly classified 78% of the individuals.

When classified by the procedure described above, the sample of 33 individuals of unknown sex was found to comprise 11 males and 22 females. The classification confirmed later field identifications of sex for all of the 5 magpies (3 males, 2 females) for whom a visual sexing attempt had been made.

Throughout this discriminant function analysis it was assumed that all measured variables could be considered, regardless of

TABLE 2.c

Results of discriminant function analysis on tarsus, toe and beak length measurements of 18 sexed magpies and 33 unsexed magpies

Actual Group	No. of Cases	Predicted Group Membership Male	 Female
Male	9	6 66.7%	3 33.3%
Female	9	1 11.1%	8 88.9%
Ungrouped	33	11 33.3%	22 66.7%

Classification Function Coefficients

Variable	Male	Female
Tarsus length	6.499376	6.280153
Toe length	4.127588	3.844738
Beak length	1.896850	1.723930
Constant	-302.8236	-272.9843

the age of the measured bird. In other words, the possibility that differences in body size due to age confounded sex differences was ignored. Since females tended to be smaller than males (see section 2.2.4), younger -and smaller- magpies would be classified as females, rendering the male estimate conservative.

It was shown above that there was a possibility that one of the classifying variables, beak length, was subject to age effects. Therefore a second discriminant function analysis was performed, with only tarsus length and toe length specified.

This time, only 67% of the cases of known sex were correctly classified, 12 birds were grouped with the males, and 21 were considered to be female. When age effects were controlled, one bird was reclassified from female to male.

The estimate that 33% of the nomadic flock birds were male and 66% were female must remain conservative however, because of the small sample sizes (n_m=9, n_f=9) from which the original function was derived.

The size of the mobile phase of the population was estimated from capture-recapture data, for the spring of 1978. The estimated population parameters are presented on Table 2.d. The estimated size of the mobile phase within the study area fell over 65 days from 242 to 36; the estimated daily

TABLE 2.d

Population parameters estimated from flock recaptures, using Fisher-Ford method

Day	Days elapsed	$\hat{N}_i$	$\hat{L}_i$	$\hat{B}_i$
1	-	-	-	-
2	17	242	24	-
3	14	118	12	33
4	9	139	14	-72
5	11	53	5	-30
6	11	18	2	20
7	3	36	4	-

where $\hat{N}_i$ = estimated population size on day i

$\hat{L}_i$ = estimated losses to day i

$\hat{B}_i$ = estimated additions to day i

and ϕ (daily survival rate) was 0.9

survival rate was 0.9.

Population density is estimated in section 2.2.4.

By mid-January 1979 most flock birds foraged on the treeless pastures at the eastern limit of the study area (see Figure 2.b). These pastures were short, grazed by sheep, and frequently bisected by deep but grassed gullies. About 20 magpies were still using this area in January 1982.

Another local concentration of mobile birds was detected on 14-9-80. More than 20 magpies of Age Class Four were recorded flying, singing and foraging in the area indicated on Figure 2.b. On 3-12-80, 28 young magpies were counted in the area but by January 1982 this flock had dissipated and the area was once more defended by sedentary magpies.

A third flock of 12 magpies was first observed 7-8-82, in treeless pasture at the northern side of the study area (see Figure 2.b). Three individuals of Age Class Four were counted amongst these animals. The fate of this flock was not documented.

Flock birds banded in 1978 were resighted in that area until June 1980. In addition, 3 flock-banded individuals were resighted as territorial residents. Two of these magpies were females or subadults in group-defended territories outside the study area, and were not individually identified.

The third bird was resighted in March and June 1980 as an adult male in company with 3 and then 2 females or subadults at the location marked on Figure 2.b. The group was attempting to establish a territory but had disappeared from that location before the census in January 1981. The bird was variously identified as 'white-blue-red' or 'white-green-red'. The former combination marked a magpie banded at Age Class Four in 1978 and identified as male by the discriminant function analysis, while the latter combination identified a flock-banded subadult (Age Class Five) scored as female in the discriminant function analysis. Depending on identity, this bird had spent between 18 and 30 months in the mobile phase of the population.

The flock birds under observation during this study did not attempt to reproduce.

2.2.3 Magpie Territories.

Approximate boundaries and dates of first observation for territories discovered in the study area are superimposed on the sketchmap in Figure 2.c. Partial histories of 30 territories have been compiled and form the data-set for section 4.2.1. Each territory is coded by number on the map.

During the course of the study, 22 territorial residents were trapped and banded in the study area. Of this sample, 12 were from Age Class Six (7 males and 5 females); 4 from Age Class

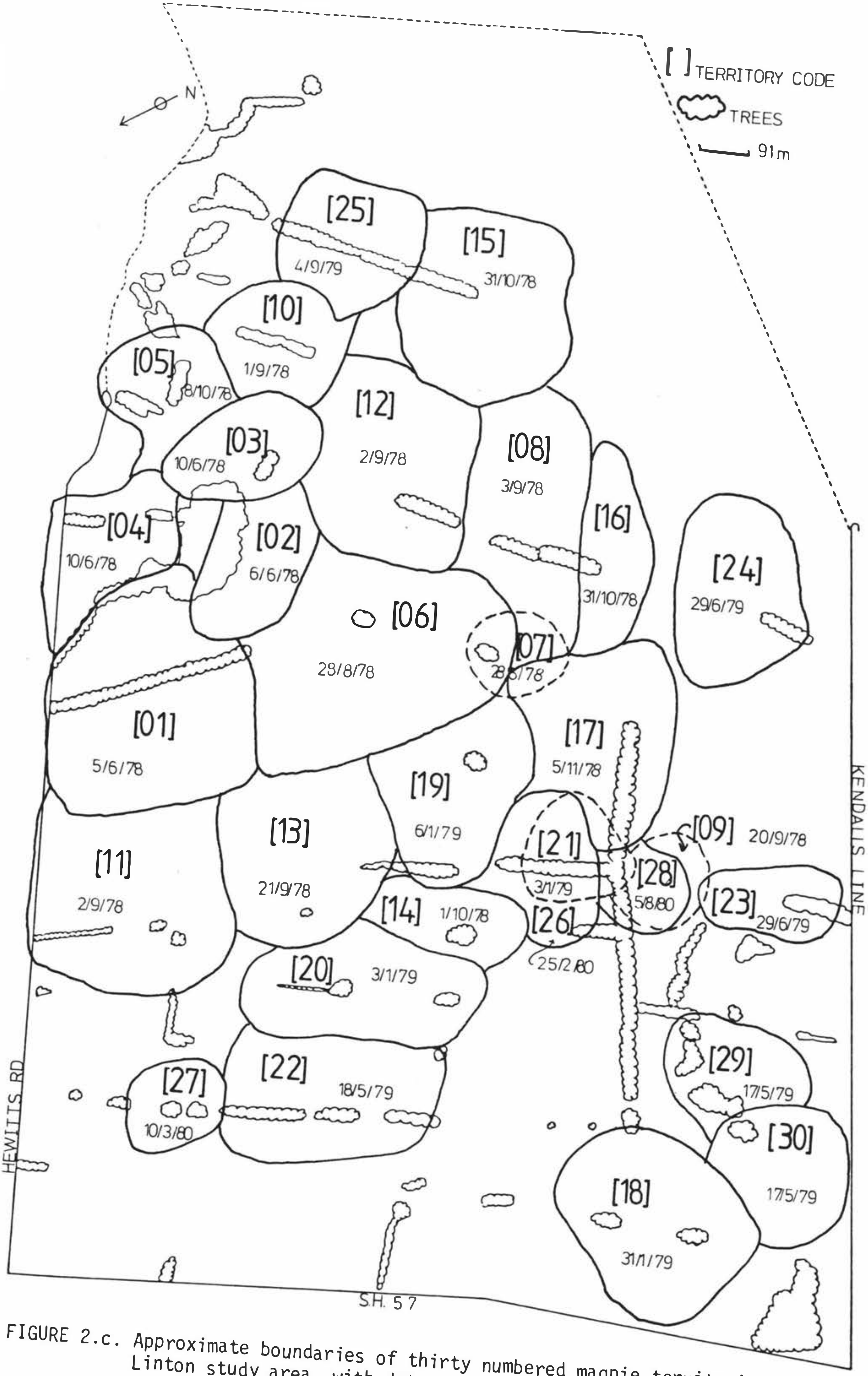


FIGURE 2.c. Approximate boundaries of thirty numbered magpie territories in the Linton study area, with dates of first observations.

Five (2 males, 1 female and 1 sex- unknown); and 6 from Age Class Three (sex unknown). Eleven of the magpies (50%) were white-backed (Colour Class A), and 11 (50%) were partly black-backed (Colour Classes B,C,D).

Six other adults trapped in territories outside the study area were added to the sample of 12 adults described above, in order to obtain linear discriminant functions for use in classifying other magpies by sex (section 2.2.2). Refer to Table 2.c above for a summary of the analysis.

Individuals of known sex from Age Class Five were added to the adult sample for comparison of morphometric measurements between sexes, by t-test. The results are summarised on Table 2.e. Males had significantly longer beaks than females, and tended to have deeper beaks although the difference was not significant.

Morphometric measurements obtained from the 6 magpies sampled in Age Class Three are summarised on Table 2.f. After t-testing against measurement means for adult females, only bodyweight was found to be significantly lighter ($P<0.05$). Territorial magpies not yet one year in age had reached adult proportions in every measure except bodyweight, but note that Age Class Four birds in the larger flock sample had smaller beaks than those in Age Class Five and Six (see section 2.2.2).

TABLE 2.e

Morphometric measurements of territorial males and females

		Male	Female	T Test $MU_1 = MU_2$
n		11	10	
Variable				
Weight (gms)	$\bar{x}$	360.0	351.0	t = 0.66
	S	35.5	26.3	
	$S_{\bar{x}}$	10.7	8.3	P = 0.52
	max	445.0	405.0	
	min	320.0	310.0	
Tarsus (mm)	$\bar{x}$	56.9	54.9	t = 1.57
	S	3.7	2.1	
	$S_{\bar{x}}$	1.1	0.7	P = 0.14
	max	61.5	58.5	
	min	52.5	51.5	
Toe (mm)	$\bar{x}$	31.9	30.2	t = 1.53
	S	2.7	2.6	
	$S_{\bar{x}}$	0.8	0.82	P = 0.14
	max	28.0	35.0	
	min	33.0	26.5	
Toenail (mm)	$\bar{x}$	12.2	11.4	t = 1.71
	S	1.2	0.8	
	$S_{\bar{x}}$	0.4	0.3	P = 0.11
	max	14.5	12.5	
	min	11.0	10.0	
Beak length (mm)	$\bar{x}$	53.1	47.4	t = 2.17
	S	4.3	7.2	
	$S_{\bar{x}}$	1.3	2.3	P = 0.04*
	max	64.0	52.0	
	min	49.0	27.5	
Beak depth (mm)	$\bar{x}$	21.3	20.1	t = 1.96
	S	0.9	1.8	
	$S_{\bar{x}}$	0.3	0.6	P = 0.07
	max	22.5	23.5	
	min	20.0	18.0	
Beak width (mm)	$\bar{x}$	17.7	17.3	t = 0.44
	S	1.7	1.8	
	$S_{\bar{x}}$	0.5	0.6	P = 0.67
	max	21.0	21.0	
	min	16.0	15.0	

where * = $P < 0.05$

TABLE 2.f

Morphometric measurements of Age Class 3 magpies

Variable	$\bar{x}$	S	$S_{\bar{x}}$	max	min
Weight (gms)	320.0	16.1	6.6	345.0	295.0
Tarsus (mm)	55.9	2.4	1.0	60.5	54.0
Toe (mm)	30.6	1.3	0.5	33.0	29.0
Toenail (mm)	11.3	1.3	0.5	14.0	10.0
Beak length (mm)	48.7	2.4	1.0	52.5	46.0
Beak depth (mm)	20.3	0.5	0.2	21.0	20.0
Beak width (mm)	18.0	2.7	1.1	21.0	14.0

The size of the sedentary phase of the population was determined by direct enumeration during four summer censuses in the study area. Although few of the territorial residents were colour-banded, individual magpies within the study area varied in the patterns of nape and back plumage and were readily identifiable. Others limped or displayed such idiosyncratic behaviour that they could be continually recognised.

From January 1979 to January 1982, 84 territory inventories were completed - 20 in 1979, 27 in 1980, 21 in 1981 and 16 in 1982 (Table 2.g). Just over half (n=48) of these counts were from 12 territories and represented a continuous record of occupancy over 36 months (Table 2.h).

A total census efficiency of 90% was achieved. (See Table One of the Appendix for confirmation).

It was found that the adult male:female ratio remained at 1:1 throughout the study, and that Age Class Three magpies made up about 30% of the sedentary summer populations. An average annual production of 0.96 juveniles per adult female was calculated from the sample of 12 regularly sampled territories.

The null hypothesis that the four annual counts were drawn from the same population was tested using Friedman's two-way analysis of variance by ranks. Each row in the analysis

TABLE 2.g

Summer census counts of territorial magpies

Year	1979	1980	1981	1982
No. territories	20	27	21	16
No. magpies	88	121	82	65
No. adult males	27	40	30	20
No. adult females	26	31	23	20
No. age class 5 birds	0	1	4	1
No. age class 4 birds	4	9	2	2
No. age class 3 birds	29	31	19	19
No. unclassed birds	2	9	4	3

TABLE 2.h

Summer census counts of 12 closely-watched territories

Year	1979	1980	1981	1982
No. territories	12	12	12	12
No. magpies	47	53	48	48
No. adult males	15	16	17	13
No. adult females	16	15	15	14
No. age class 5 birds	0	1	3	1
No. age class 4 birds	2	3	1	2
No. age class 3 birds	14	18	11	15
No. unclassed birds	0	0	1	3

represented a matched set of subjects (Age Class Six males, Age Class Six females, Age Class Five birds, Age Class Four birds and Age Class Three birds) from the 12 territories, and the columns represented the four census counts. The scores in each row (proportion of the annual count in a given age/sex class) were ranked from lowest (1) to highest (4), and Friedman's test was used to determine whether the rank totals in each year differed significantly. A value of X=0.42 was obtained, causing the null hypothesis to be retained. The numbers of magpies in each age and sex class did not vary significantly from year to year.

The total sampled population ranged in size from 65 magpies in January 1982 (16 territories) to 121 birds in January 1980 (27 territories). Density estimates were prepared from these data in section 2.2.4.

No data on longevity were collected during this study, but the mean survival rate of adults in the 12 territories monitored for 36 months was estimated to be 0.85. A total of 35 adults contributed 1067 magpie-months to the survival data, and causes of "death" (disappearance from a territory) were not known.

2.2.4 Magpie Dispersion in the Study Area.

Population size estimates were prepared separately for each of the two population phases. The estimated numbers of mobile birds on flock grounds in the spring and early summer of 1978 were summarised on Table 2.d above, and the counted numbers of sedentary magpies in territories were given on Table 2.g above.

The size of the study area was found from the calibrated aerial photograph to be 3.03 km^2 (303 Ha.). That part of the area observed to be used by mobile magpies between September 1978 and January 1982 and called the 'flock grounds' measured 0.35 km^2 (35 Ha.), and was just over 10% of the total studied area. The initial density of flock birds in 1978 was 242/0.35 magpies per square kilometre, or 7 birds per hectare. Sixty five days later, density had fallen to 1 magpie per hectare.

Several instantaneous density estimates for the territorial phase were prepared. Approximate sizes of 30 territories were found from the aerial photograph and used for the density calculations. In January 1979, 88 birds were counted in 20 territories with a total area of 1.2 km^2 (124 Ha.). The density was 0.7 territorial magpies per hectare. The average density over 4 years from the 12 continuously censused territories (area 71.5 Ha.) was 0.7 birds/Ha., and the density calculated in 1980 (when 27 territories were counted over 146 Ha.) was 0.8.

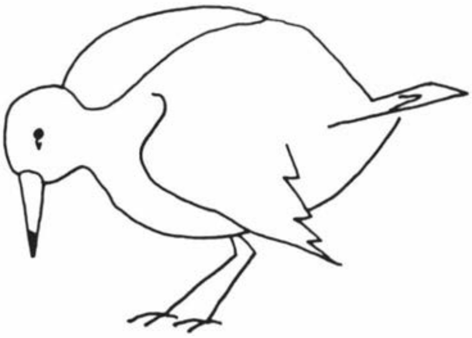
There was no correlation between the number of birds per territory and territory size (r_s=0.226, n=12, P>0.10).

The pattern of distribution of the territorial phase was calculated from nearest neighbour distances between territory nexuses. The mean observed distance to the nearest neighbour was 229.8m, while the mean expected distance was calculated to be 103.5m. For this distribution, R=2.22, equivalent to a distribution in which the mean distance to the nearest neighbour (the nexus of the next territory) is maximised. The centre points of individual territories were uniformly distributed.

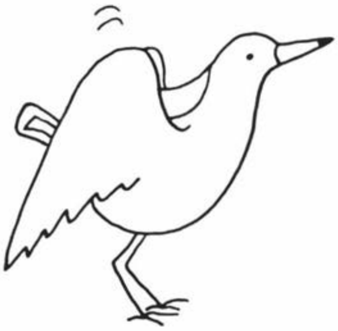
2.2.5 Stereotyped Display Behaviour.

Ad libitum records of the performance of stereotyped action patterns by magpies covered four social contingincies: (1) interactions with conspecific competitors, (2) interactions with mates (see section 4.2.7), (3) interactions with young (see sections 4.2.6 and 4.2.9), (4) interactions with peers (see section 3.2.3). Three displays performed in the first context are described here.

Birds engaged in inter- and intraterritorial disputes were often observed to adopt a hunched posture, with feathers fluffed out and bill down. Walking was stilted and frequently interrupted by bouts of intense pecking at the ground. This posture is illustrated on Figure 2.d, and was termed "bill-down" display. This display was associated with other aggressive acts by adult magpies and was considered to perform a threatening function.



BILL-DOWN DISPLAY



WING-TREMBLING DISPLAY

FIGURE 2.d. Stereotyped display behaviour of magpies.

In similar social interactions, magpies were sometimes observed to stand or run with the wings outstretched and trembling rapidly (Figure 2.d). This action was performed repeatedly during the spring of 1979 by a subordinate female attempting to reproduce in territory [12], whenever she was approached by the dominant hen. This and other observations led to the conclusion that the "wing-trembling" display functioned in appeasement.

The third display was performed by magpies flying over territories in which they did not land. The birds "tilted" in flight from side to side, so that the plumage of the back was clearly visible to the observer. A function for this display could not be determined, nor could general rules for its performance.

2.2.6 Singing Behaviour.

It was only possible during this study to make general observations of the type and timing of vocal displays. Magpies vocalised in defence of resources, during alarming incidents, in and at nests, and in less obviously functional ways (such as soft subsong by younger birds).

The group singing which characterised magpie occupancy of territories was too complex for analysis without sound recording equipment, but seemed to the observer to include a terminal 'flourish' and to involve duetting.

Alarm calls were either two-note vocalisations repeated until the alarm was over, or a single thin whistle which was difficult to localise and usually performed towards evening.

Captive-reared magpies began sub-song at about 4 months of age and continued to warble quietly to themselves at intervals for several years. Sub-song was most often heard in the field near noon on warm and windless days.

Incubating females were heard to beg from nests (see section 4.2.8), and adults participating in nestling care vocalised softly to the younger birds. From fledging to achievement of independence (4 months of age), magpies elicit food-exchange from adults by vocalising repeatedly and loudly.

2.3.0 Discussion

The existence of numerous nonterritorial and nonreproductive individuals within a magpie population was first described by Carrick (1963). Flock birds were viewed as a nonmigratory overflow from the territorial population, able to exist because of the generalised diet and versatile foraging behaviour of the species. This study has confirmed that a nonterritorial phase constituted part of a New Zealand population. Independent young in populations of the Western magpie may live in small groups in neutral zones between nesting territories, and displaced adults may travel through defended areas, but the occurrence of large aggregations of nonbreeding animals has not been reported (Robinson 1956).

Each of the nonterritorial flocks which formed in the study area was first detected in August or early September, a time period corresponding to breeding by territory holders (see section 4.2.2). Also, many of the flock members were magpies judged by plumage appearance to be aged between one and two years (Age Class Four). These observations suggest that flocks were formed from dispersing juveniles which had migrated from the territorial phase of the population, and that emigration from territories took place just prior to the fledging of the next cohort of chicks.

The estimated change in size of the flock which formed in Spring 1978 demonstrated that emigration from territories was simultaneous, and led to an initial period of dispersal by the younger magpies. The mobile birds may have returned to natal territories or settled outside the study area, before the flock stabilised at about 35 individuals. The degree of flux within the flock after formation was unknown, but banded individuals were still present on the flock grounds 18-20 months later. A restricted home range may enable "floaters" or nonterritorial individuals to accumulate knowledge of the terrain and to form bonds of attachment and identification with other animals (Smith 1978).

At least one-third of the magpies trapped in the flock were male, based on morphological measurements. More males than females of known sex (3/9) were incorrectly grouped by the discriminant function analysis so that 33% of the initial male sample was identified as female. If 33% of the flock sample of males was incorrectly assigned female grouping, then the actual number of males in the flock sample was about 16. This figure would generate a flock sex ratio of 16 males to 17 females, or parity. In this study then, the proportion of male magpies in the flock was between 30-50%. Males comprised 61% of the flock birds studied in Australia (Carrick 1972), although the method of sexing was not described. If these sample differences reflect true population differences in flock sex ratios between Linton and Canberra, then relatively more females migrate out of the territorial phase in the New Zealand population, or the rate of recruitment of females from the flock is slower.

The territorial population density measured at Linton was four times greater than at Canberra. Although Carrick (1972) offered contradictory density estimates, on average 48 territorial magpies were counted per square mile (259 Ha). The resulting density of 0.18 territorial birds/Ha. should be compared to 0.7 birds/Ha. measured at Linton. The density of flock birds at Linton was 1 bird/Ha. after December 1978, compared with 0.15 birds/Ha. at Canberra. In other words, each hectare of foraging substrate available to nomadic birds at Linton supported 6 times more magpies than did a comparable area at Canberra. Although flock density was marginally higher than territorial density at Linton, the reverse was the case at Canberra, leading to the conclusion that Linton magpies experienced relatively less stress in the transition from territoriality to nomadism (assuming that density estimates reflected the carrying capacity of the flock and territory areas).

Of the 30 territories investigated during this study, 27 proved to be permanent and all-purpose in nature and did not overlap spatially. The remaining 3 were of short tenure. The grades of territoriality described for the Australian population (Carrick 1963) were not observed at Linton. This point is discussed fully in section 4.3.0.

The measurement of morphological characters of 18 territory residents revealed that males possessed longer and deeper bills than females and that apart from plumage differences, these were the only differences in visual appearance between the sexes. Any competitive advantage experienced by males in foraging was not reflected in significant differences in body-weight, and possible differences in male and female diets were not evaluated during this study.

Both sex ratios and population size in 12 regularly monitored territories remained static during this study. Males and females were equally represented in the territorial phase, whereas at Canberra females outnumbered males 57:43 (Carrick 1972). The differences between the two populations may indicate that subadults were incorrectly sexed as females in the Australian study, or that polygyny was more common there.

Linton territories tended to be smaller than those studied at Canberra ($\bar{x}_L$=5 Ha; $\bar{x}_C$=9 Ha) and as at Canberra, no correlation could be found between territory size and number of occupants (Carrick 1972). Shurcliffe and Shurcliffe (1974), working on white-backed magpies at Adelaide found that group size and territory size were positively correlated, but Hughes et al (1982) could find no correlation for a population of magpies at Brisbane, even when territory quality (indexed from the measured areas of short grass) was included in the analysis. Hughes et al tested three hypotheses about the relationships between territory size, territory quality and group size, and concluded that there was some evidence to favour a "food-maximiser" hypothesis, in which magpies maximised energy gain relative to the costs of maintaining a territory. Linton territories were dispersed uniformly, consistent with the hypothesis that territory occupants attempted to space themselves as far as possible. Thus, territory size at Linton appeared to be the outcome of anti-social behaviour between the different groups of occupants, rather than a reflection of the foraging requirements of individual birds.

The productivity recorded at Linton (0.96 juveniles/female) was 70% greater than at Canberra (0.56 juveniles/female). This difference may have resulted from the different availability of food evidenced from density estimates; reduced nest or fledgling predation in New Zealand; or lower levels of female-female interference (see section 4.2.6) mediated by a better food supply and a balanced sex ratio at Linton.

Although not described before for white-backed magpies, the bill-down, wing-trembling and tilting flight displays have all been observed in interactions between Western magpies (Robinson 1956). The tilting flight display was performed by males between February and November in the Western Australian study, and variants of bill-down (called the 'defiant' display) and wing-trembling (called 'lyre-wing' and considered submissive) were also described.

Inhabitants of the study area were white- and black-backed magpies. Although 25% of the flock sample was black-backed (Colour classes B,C,D), the proportion of melanic individuals in the territory sample was 50%. However it should be noted that the territory sample was small, and concentrated in locations where family members (birds of similar colour) were likely to be caught together. Despite the measurable level of melanism at Linton, the birds were considered to be conspecific.

CHAPTER THREE

Flock Cohesion and Time-Activity Budgets

3.0.0 Introduction

Birds prevented from site attachment and resource defence by the aggressive behaviour of conspecifics have two options available to them. They may aggregate with other individuals into flocks on undefended areas, or they may live singly in an "underworld" environment (Smith 1978). In common with great tits (Krebs 1971) and the Santa Cruz Island jay (Atwood 1980), nonterritorial magpies form flocks in habitats unsuitable for breeding (Carrick 1972, and section 2.2.2).

Most recent research into flocking behaviour has emphasized the advantages to individuals in terms of increased foraging efficiency and reduced predation risk (Thompson et al 1974, Caraco 1979a and b, Barnard 1980), and improved information about scarce and patchy food (Clark and Mangel 1984).

However, since the flocking phase formed a numerically small subset of the magpie population at Linton and was the outcome of emigration from the territorial units, the focus of this study was rather different.

Here, several questions were asked about the movements and day-to-day maintenance behaviour of individuals in the Linton flock, in order to develop a behavioural profile of the flock "lifestyle" (see section 5.3.0 for an explanation of the term "lifestyle").

First, was the flock a random assemblage of all the nonterritorial individuals in the study area, or did individuals associate preferentially with others? Both Ekman (1979) and Ficken *et al* (1981) showed that the membership of winter feeding flocks in small passerine species was coherent, and that attachments between flock birds led to later pair-bonding. By contrast, wintering sanderlings formed open (but nonrandom) groups with loose inter-individual bonds (Myers 1983). The two indices used to detect associations in these studies led to high association scores for individuals seen rarely and therefore were not applicable to this study. Instead, goodness-of-fit between the distribution of possible pair sightings and the Poisson distribution was investigated.

Next, did flock membership change on a seasonal or daily basis? Since individual presence or absence could not be continually monitored, gross changes in flock composition had to be inferred from changes in flock size. An investigation of the effects of month and time on magpie numbers was therefore conducted, using analysis of variance procedures.

How did flock birds spend their time? Frequent scans of the flock yielded information about the proportions of birds engaged in each activity, and the foraging portion of these data was inspected for patterns arising out of seasonal and daily influences.

Was foraging behaviour affected by the number of birds present in the flock? Since predation risk was nil during the period of study, the foraging behaviour of the flock magpies was not constrained by risk-avoidance behaviour. Any changes in the relationship between the two parameters would reflect social or prey-population changes alone, so regression analyses of flock size and proportion foraging were performed.

Finally, did flock birds have time for non-maintenance activities? If so, emigration from territories may not have been life-threatening, and opportunities to exploit territorial vacancies were not precluded by unfavourable time budgets.

3.1.0 Methods

3.1.1 Trapping and Banding

Flock birds were trapped from September 1978 to February 1979 using the technique described in section 2.1.2. A total of 33 flock magpies were individually marked with a 3-colour combination of leg bands (see sections 2.1.4 and 2.2.2).

3.1.2 Sampling behaviour

The time budget samples were obtained at 14 day intervals from September 1978 to August 1979, during complete dawn-to-dusk watches from a hide. Attempts to record individual time-budgets by following the activities of banded birds failed, because the magpies moved out of visual range frequently.

Instead, the visible flock birds were scanned each 5 minutes and a count was made of the total numbers of birds present, and the numbers engaged in each activity. The day was divided into six time periods following the method described in section 4.1.2.

3.1.3 Behaviour patterns

The observed behaviour of the flock magpies fell into seven classes of activity as follows:

(1) Foraging. Prey were obtained by walking and striking at ground invertebrates, and by pecking at insects on the sides of fenceposts. During the first month of the study, September 1978, magpies were scored as foraging if they were seen to peck during the scan count. This criterion was relaxed in the following months, and birds walking and watching the ground were also scored as foraging.

(2) Perching. The flock birds interrupted foraging bouts to perch on fenceposts and power pylons in the area. Preening

and singing were sometimes performed while perching.

(3) Standing/sunbathing/bathing. Flock birds spent extended periods of time standing on the ground without foraging. In practice it was sometimes difficult to distinguish the two activities, and the score given during a scan reflected the observed inactivity of an animal during the preceeding 5 minute interval. While on the ground and not foraging, these birds also sunbathed and waterbathed (in puddles).

(4) Flying. The number of magpies in the air over the flock area during each scan was noted. Flock birds also flew in response to disturbance from farmers and harrier hawks (*Circus approximans*).

(5) Fighting. Fights erupted between individuals and small groups, and involved short chases and aerial combat. Fights were of short duration and were usually over in 60 seconds.

(6) Playing. Flock magpies played together in mock fights, wrestling matches, and tugs-of-war. Play was initiated when a magpie crouched behind another individual and vocalised softly, or gently tugged its tail feathers. Short rushes towards another bird also led to a play interaction. Play bouts were prolonged (up to 30 minutes) and often led to several birds lying on their backs on the ground. Play was most commonly performed by Age Class Three and Four magpies.

(7) Anti-predator behaviour. Flock magpies sometimes attacked harrier hawks in the area, and alarm calls were given when hawks flew nearby.

3.2.0 Results

3.2.1 Associations between magpies.

17 of the 25 magpies banded in the flock before 25-10-78 were seen again before mid-May 1979. Of the 300 possible combinations of seeing two birds together, 69 (23%) were obtained. The distribution of pair-sightings is shown on Table 3.a, and was found to fit a Poisson distribution (P=0.05). The population of pair-sightings was therefore random, indicating that flock magpies did not have preferred associations.

Figure 1 of the Appendix has the original data on which this analysis was based.

3.2.2 Time-activity distributions.

The data set for the study of flock time budgets was collected over 250 hours of real time, and when analysed, allowed the following statements to be made. (See Table 3.b for a summary of the sampling effort).

The number of birds counted in the flock at 5 minute intervals

TABLE 3.a

Distribution of possible-pair sightings

Possible-pair sightings	0*	1	2[†]	3
No. of pairs recorded	231	62	6	1

* for example, possible-pair never seen

[†] for example, possible-pair sighted twice

TABLE 3.b

Flock time budget sampling effort

Month	No. of scans	mean birds/scan	median birds/scan	max birds/scan	min birds/scan
September	125	48.5	50	77	11
October	169	16.3	16	34	1
November	335	21.5	20	79	0
December	349	11.9	10	38	1
January	347	15.4	10	51	1
February	322	17.3	17	36	1
March	231	14.5	13	43	1
April	277	20.4	20	46	3
May	364	18.5	19	42	2
June	120	20.8	21	35	4
July	182	17.4	17	31	5
August	102	16.2	17	26	6

varied significantly with month and time of day (Table 3.c), and there was also a significant interaction between the effects of months and time periods. Figure 3.a illustrates flock sizes during the study. No obvious patterns could be discerned.

The transformed proportions of foraging birds varied significantly with month but not time of day (Table 3.d). However there was a significant interaction between the effects of month and time on the proportion of the birds in the flock foraging, indicating that any influence of time on foraging behaviour depended on the month of the year. The strict criterion used to judge whether or not birds were foraging in September (the first month of the study) led to very low foraging proportions, so September was omitted from the analysis and the criterion was relaxed for future months.

A positive correlation between the number of magpies present and the number foraging was discovered for all months, but the September and December results were weak. The correlation coefficients, regression line intercepts and coefficients of determination are listed on Table 3.e. The amount of explained variation (R^2) improved for June and August when the foraging numbers were normalised. The value of the intercept may be interpreted as the number of magpies present before foraging began, and was thus an index of the foraging drive of the magpies in the flock area. If the birds were hungry, then foraging was predicted to begin with fewer birds present.

TABLE 3.c

Analysis of variance on number of flock birds per scan, by month and time, excluding September

Hypothesis	Calculated F	df	Critical F ($\alpha_{(2)} = 0.05$)	Decision
1*	38.315	10	2.05	reject H_o
2†	11.376	5	2.57	reject H_o
3††	14.309	50	1.43	reject H_o

* the number of magpies per scan was the same for all months

† the number of magpies per scan was the same for all time periods

†† differences in the number of birds per scan between months were independent of time period differences

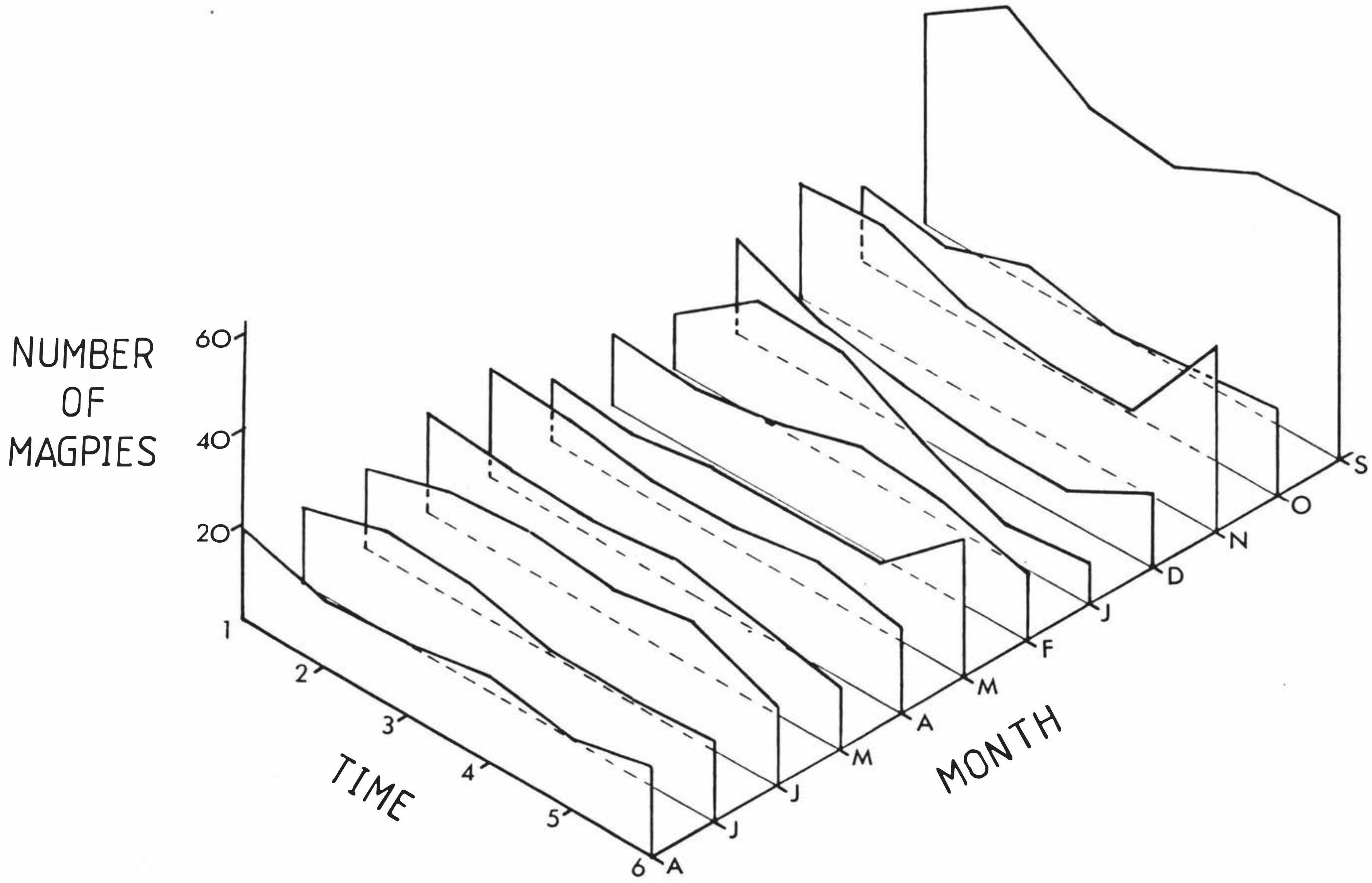


FIGURE 3.a. Variation in flock sizes measured during six day-time periods for twelve months.

TABLE 3.d

Analysis of variance on transformed proportions of flock magpies foraging, by month and time, excluding September

Hypothesis	Calculated F	df	Critical F	Decision
1*	25.976	10	2.05	reject H_0
2†	1.746	5	2.57	accept H_0
3††	4.080	50	1.43	reject H_0

* the proportion of magpies foraging was the same for all months

† the proportion of magpies foraging was the same for all time periods

†† differences in the proportion of magpies foraging between months were independent of time period differences

TABLE 3.e

Regression analysis of flock size and foraging activity

Month	r	Intercept	R^2
January	0.910	5.37	82.8
February	0.795	6.98	63.1
March	0.937	2.74	87.7
April	0.698	9.39	48.5
May	0.676	9.78	45.6
June	0.526	15.7	27.1
June*	0.531	12.5	28.4
July	0.511	12.0	25.7
August	0.732	7.99	53.1
August*	0.735	16.2	53.5
September	0.425	-	-
October	0.758	7.85	57.3
November	0.763	12.6	58.1
December	0.435	-	-

* normalised scores

The percentage of birds foraging and performing other activities in each month and time period is shown on Figure 3.b. Anti-predator behaviour was so infrequent that it disappeared during the conversion of the original counts to percentages. The months with smaller regression intercepts (January, February, March) did not perfectly predict months in which the greatest proportions of birds were foraging throughout the day (February, March, April). In April for example, foraging percentages were high but around 9 birds were present before foraging began.

The proportion of birds foraging in the early morning time period tended to be low and counterbalanced by the proportion perching in the vicinity. In most months foraging activity intensified as the day progressed.

More of the flock birds stood or sun- and waterbathed in November, December and January but these activities decreased as the percentage of animals foraging increased. When foraging activity began to decrease again in May, more birds were scored as standing.

Flock birds were seen to play only during afternoon time periods in November, December, March, July and August.

3.3.0 Discussion.

The magpies banded in the Linton flock did not show

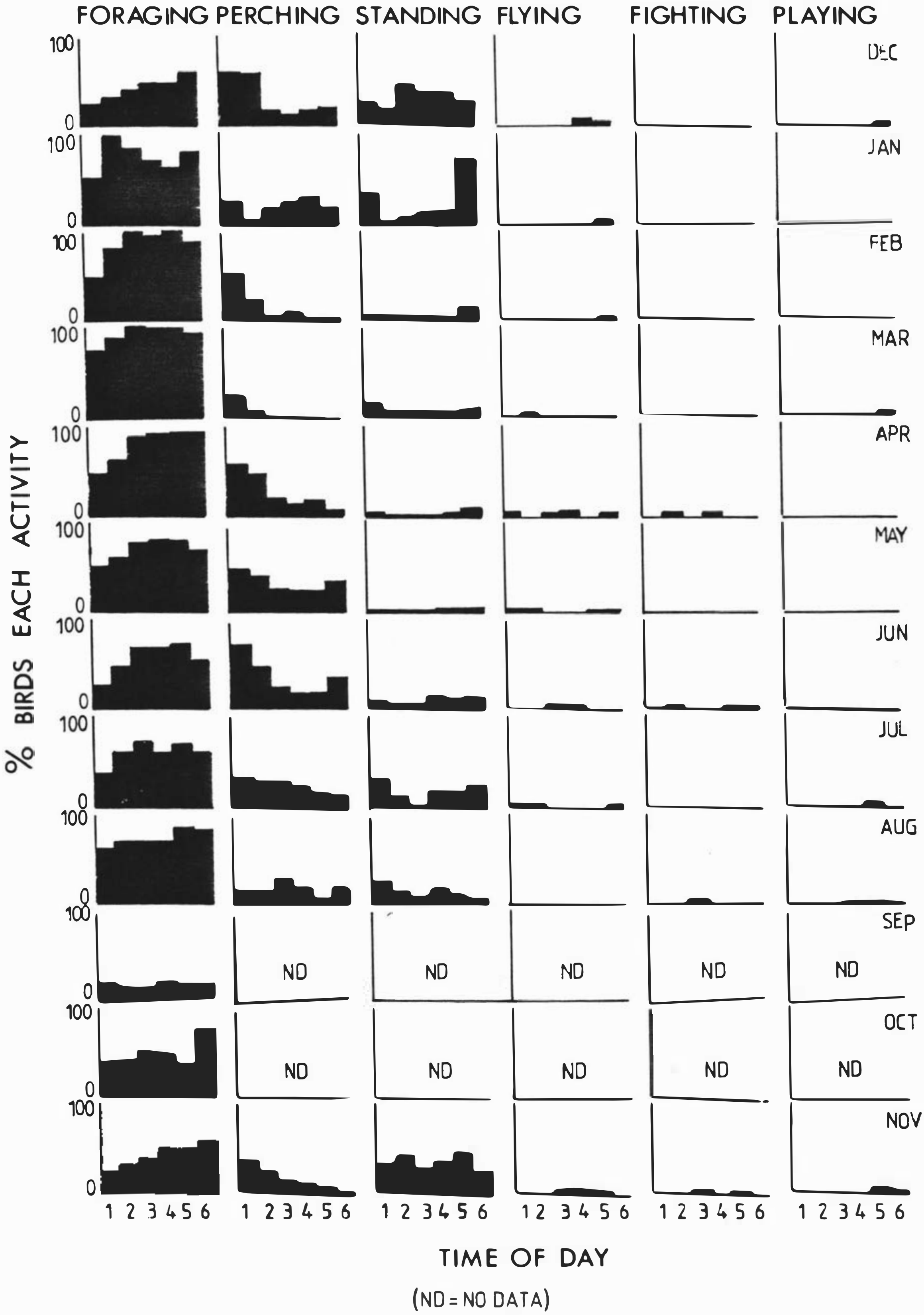


FIGURE 3.b. The percentage of flock magpies performing each activity during six day-time periods for twelve months.

preferences for associating with each other, leading to the conclusion that the flock was not a coherent, highly organized social group. Social interaction between flock birds took the form of fighting or playing, and there was no observational evidence for a social hierarchy. Carrick (1972) described flock magpies as "locally nomadic over all the treeless pasture" in his study area, but no information about the local movements of birds was obtained at Linton. In the Canberra study, one quarter of the new territorial groups contained magpies known to have been together in the flock (Carrick 1972). At Linton one flock-banded magpie was observed to make a territorial attempt (section 2.2.2), and displaced territory holders have joined the flock (section 4.2.3). The magpie flock was a loose assemblage of birds at least temporarily prevented from being territorial.

The flock varied in size with month and time of day. As shown on Figure 3.a, flock sizes fluctuated over short intervals indicating that flock membership changed frequently. While mid-morning numbers may have been influenced by the movements of territorial juveniles from March, other changes could not be accounted for. Now that variable flock composition has been established, the daily movements of individuals need to be tracked in order to study interactions between magpies from different flock areas, and between flock and territorial magpies. In the communally breeding Western magpie, no significant nonterritorial component exists (Robinson 1956), and nomadic individuals make inter-territory movements.

PLATE 3.a. Flock magpies perching, preening and foraging.

The primary activity of magpies in the flock area was foraging, and a higher proportion of the birds foraged in February and March than in other months. Seasonal variations in prey availability may be inferred from these changes in the relative proportions of birds foraging, perching, standing and interacting socially. If social patterns do not alter when foraging levels change, then foraging must have been influenced by changes in the food supply (assuming that metabolic needs remain similar). Thus from the time budget data, February and March were months of reduced prey availability.

The number of magpies foraging increased linearly as the flock size increased. Flocking therefore neither inhibited nor enhanced foraging behaviour. However, the linear model accounted for only one quarter of the variation in June and July, pointing to a more complex interaction between flock size and foraging activity in the winter. As well, the regression intercepts for these months were high, so that a 'critical mass' of magpies was reached before foraging began. In December more of the flock birds were inactive than in other months and foraging was only weakly correlated with flock size. The lowest regression intercept was obtained in March, when foraging occupied most of the flock birds at any time. This lends support to the idea that flock magpies experienced a food shortage in the autumn.

Except for the autumn months, between 5 and 45% of the flock were standing inactive at any time (see Plate 3.a). Some birds also fought or played together. Obviously ill magpies were never seen in the flock and an overall subjective impression of healthy unstressed animals was obtained. The daily survival rate was estimated in spring 1978 to be 0.9 (section 2.2.2). At Canberra however, flock birds succumbed to predators and diseases and had lower survival rates than their territorial counterparts. Flock birds also had lower bodyweights than the territory holders (Carrick 1972). Insufficient territory birds were trapped at Linton for a comparison with the flock birds, but based on the qualitative criteria above, the Linton flock birds experienced better living conditions than those at Canberra.

CHAPTER FOUR

Territory Histories and Time-Activity Distributions

4.0.0 Introduction

A variety of behavioural mechanisms have evolved in response to conspecific competition for access to resources limited in space and time. Brown (1964) argued that intraspecific aggression in response to competition should lead to territoriality when the area is 'economically defendable' (and territory is "an exclusive area" (Schoener 1968), but see section 2.3.0). Subsequent studies of the costs and benefits of territoriality were reviewed by Davies (1978).

The first attempt to construct a quantitative theory of territoriality was undertaken by Pyke (1979) and focussed on optimal territory size. He hypothesized that "an animal which is defending a territory will adopt a territory size and time budget which maximize its Darwinian fitness (i.e. which are optimal)",and formulated a model for nectar-feeding birds based on minimization of daily energy cost rather than maximization of resting time. A plethora of optimal feeding-territory size models followed and were reviewed by Schoener (1983), who examined the effects of changes in major environmental factors (such as food density and intruder pressure) on predictions by the models. For the time-minimizing models, feeding time and defence time were positively related and for one energy-maximising model they were negatively related, allowing the two strategies to be separated in the field.

Optimal territory size may be influenced by extrinsic factors such as the number of competitors. Verner (1977) postulated that defense of more resources than needed for reproduction would prohibit conspecifics from breeding, thereby enhancing the fitness of the 'spiteful' territory holders through interference competition (the 'superterritory' concept). Both Colgan (1979) and Getty (1979) discounted the possibility, based on Maynard Smith's (1974) concept of evolutionary stable strategy (ESS) and a genetic model respectively. However, Parker and Knowlton (1980) used two frequency dependent (ESS) models to investigate the effects of interactions with competitors on the evolution of territory size, and found that superterritories may evolve when some animals are excluded from resources (the alternative was that resources be shared unequally among all individuals), and the potential fecundity of individuals is low. Burger (1981) suggested that defense of a larger than necessary territory could have a direct effect on the fitness of the territory holder by decreasing the likelihood of predation.

In nature, the same territories may be defended by more than one individual. Competitors thus become cooperators and hypotheses about the evolution of territory size must be harnessed to a consideration of the evolution of sociality.

Both spatial and temporal dispersion of resources potentially influence toleration by conspecifics of each other. Waser (1981) summarised earlier studies of group size in relation to food patch (or feeding-territory) size, and developed a model of sociality for small African carnivores in which the costs of tolerating conspecifics were a function of the rate of resource renewal.

The influence of the dispersion pattern of carcases on group size and territory size for the brown hyena (Hyaena brunnea) was investigated by Mills (1982), who concluded that territory size was related to the distribution of food but group size was related to the quality of the food (size of carcases) in the territory.

Recently von Schantz (1984a) predicted that "non-migratory animals living in an environment where the resources fluctuate should have a constant territory size if the animals life-span is longer than the average time period of the resource fluctuations". Such obstinacy would permit group size to increase when resources are super-abundant, through the retention of offspring. This appeared to account for fluctuations in red fox (Vulpes vulpes) group size (von Schantz 1984b).

In his Canberra study, Carrick (1972) found that magpies divided the pasture and woodland into territories which varied in their size, quality and permanence. Most territorial groups originated in the flock as open groups which monopolised good feeding areas. In some cases the group members associated only during daytime, and roosted separately. The defended areas had no trees and endured on average for 8 months. About one-third of these 'open territories' were occupied by male-female pairs and the remainder were defended by groups. Nest sites were absent and females in open groups did not breed. Magpies living in mobile groups commuted between an outer feeding area and a very small inner group of trees. From 36 complete mobile group records it was found that these territories also had a mean duration of eight months. Eighty percent of the sample comprised groups of more than two birds. Although females attempted to breed, they were never successful. The marginal territories were of two sorts. Inner marginal territories were small areas of poor pasture surrounded by trees and compressed by neighbours. In contrast outer marginal territories covered large feeding areas, with few low trees or bushes. Most marginal territories were defended by pairs or groups weighted in favour of females, and lasted on average for 11 months. An average annual production of 0.09 juveniles/female was recorded. Permanent territories encompassed enough pasture and trees to support both survival and an average production of 0.56 juveniles/female. They were long-lasting; tenure ranged up to 133 months, and a mean duration of 47 months from 159 histories was calculated.

Not only territory type but also group composition varied at

Canberra. The significance of this phenomenon was lost at the time of publication because the work was aimed at supporting Wynne-Edwards (1962) thesis that population size is regulated by territoriality and was presented as a population-level study. The group-territoriality described by Carrick has been interpreted as an example of cooperative breeding (see section 6.0.0) and an opportunity to examine intraspecific variation in social systems (as defined by Lott (1984)) was lost. The paradox of cooperation in a competitive system has yet to be examined for magpies.

The aims of this chapter are to describe the responses of magpies to competition for resources in a New Zealand setting, and to investigate the consequences of variations in social behaviour for individuals.

After an outline of the annual cycle of activity in the territorial phase of the Linton study population, the interactions between and within territorial groups are described.

Then, within-group behaviour is analysed in terms of time-activity distributions. Also called time budgets (see for example Orians 1961), such records focus on the timing of, and amount of time expended in each activity performed by focal animals. The underlying rationale of a time budget study is that even subtle differences in the expenditure of time and energy can affect reproductive success (Orians 1961).

Traditionally, researchers have sought to describe the 'best' or optimal time-budget under various conditions (Verner 1965, Wolf and Hainsworth 1971, Pyke 1979, Turner 1979), but it has been suggested that animals may manage risk more effectively by feed-back or feed-forward mechanisms (Rollo et al 1983), or use satisficing strategies (Herbers 1981) which do not invoke optimization.

Here, a large sample of time-activity records was collected and examined systematically in order to answer the following questions. First, was behaviour (measured as the time expended in an activity) influenced by month or time of day? Data from 9 adult magpies were examined for the answer. Each of the major behaviour classes was then investigated, in order to discover month and time influences on performance. Next, were there differences between individuals in the time apportioned to each activity? By checking individual plots of the fitted values versus their residuals after the variance analyses, it was possible to identify months and times when some animals differed from the others in their behaviour. The original scores for the uncommon classes of activity were also graphed, to check for individual differences.

Throughout the time budget analysis, the aim was to reduce a large volume of real-time data to a few simple statements about the ways in which territorial magpies in pairs and groups apportioned their time, so that the significance of territoriality in their lives could be understood.

4.1.0 Methods

4.1.1 Trapping and Banding.

Territory occupants were trapped and colour-banded using the methods described in sections 2.1.2 and 2.1.4. During this study 22 territorial residents were individually banded, and remaining birds were identified by variations in plumage, or idiosyncratic behaviour (see section 2.2.3).

4.1.2 Sampling Behaviour.

Territories were regularly checked for the presence or absence of magpies (see section 2.1.7) and ad libitum records of especially social behaviour were made during these visits (see section 2.1.9).

From September 1978 to August 1979 three territories containing a total of 9 magpies were sampled for time-activity distributions. Two of these territories ([01],[06]) were defended by monogamous pairs and the third ([08]) was defended by a group composed of 3 males, 1 female and 1 Age Class Five bird which was later discovered to be a female. Reproduction did not take place in [08] during the study and no time budget samples were taken in that territory in September. Incomplete records were collected from two other territories of short tenure containing 7 individuals of all ages.

Each sampled territory was visited at 14 day intervals, and sampled for a complete day from dawn to dusk. Observations were conducted from a hide erected in the territory the previous day, and facilitated by the use of 10x40 binoculars (Zeiss).

A focal subgroup sampling regime was employed, in which every territory occupant was kept under continuous observation during the sample period of up to a complete day (Altmann 1974). Thirteen distinct classes of activity were distinguished on functional criteria (see 4.1.3) and the behaviour state of each individual was scored each minute. Except when birds were provisioning nests, the durations of behaviour states were recorded to the nearest minute. When a transition to another activity occurred, the minute in which the transition happened was added to the total duration of the subsequent state. When a magpie in the group under observation was out of sight for a short period, the behaviour seen when the bird reappeared was scored in the out-of-sight period (Lehner 1979). If the out-of-sight period was long relative to the duration of the most common behaviour states, then category "unknown" was scored.

Following the method of Verner (1965), days were divided into six approximately equal parts, using noon as the mid-point. In this way seasonal differences in day length were converted into more-or-less similar time periods. Dawn and dusk were judged subjectively. Behaviour scores for each individual were summed within time periods in each month. Appropriate corrections were made for New Zealand Summer Time.

The analyses of these data are described in section 4.1.4.

4.1.3 Behaviour Categories.

Thirteen different classes of activity were recognised in the time-activity study. When activities were not functionally exclusive, a subjective decision about the dominant activity was made. For example, a bird walking and occasionally striking a prey item was scored as "foraging".

Behaviour patterns with a common function were classed together as follows.

(1) Foraging. All actions which led to successful prey capture were scored in this category. They included walking and striking, digging with the bill, turning over objects, and hawking from trees or fenceposts. Predation on small vertebrates was rare but included in this category, and consumption of plant material was never observed (but see Carrick 1972 and Vestjens and Carrick 1974).

(2) Perching. Magpies perched in trees, on fenceposts, on buildings and on powerlines in their territories. Foraging bouts were interrupted by periods of perching on fenceposts near the feeding site, and longer periods of perching were

generally spent in trees. Perching behaviour may have been multi-functional, contributing to both rest and surveillance.

(3) Territory Defence. This category included singing behaviour but not alarm calls or subsong. Defence involved both static and aerial displays, and fighting, as described in section 4.2.3.

(4) Maintenance. Preening, sunbathing and drinking actions were grouped together as maintenance behaviour. The term maintenance is not used here in a functional sense, but as a catch-all for activities directed by the actor at the self.

(5) Antipredator. All responses to potential predators were scored in this category. Although magpies were never observed to be preyed upon at Linton, they responded with vigorous singing and attacking whenever the territory was entered by a swamp harrier (Circus aproximans) or a human.

(6) Within-group Social Interactions. The duration of interactions with other occupants of the territory were timed, and the identity of the actor and reactor were noted. Social interaction records were extracted from the time-activity data to form a separate all-occurences sample. Play behaviour was not included in this category.

(7) Play. Actions interpreted as play are described in section 4.2.6. Play was performed by both adults and younger

magpies, and typically consisted of boistrous wrestling on the ground, aerial chasing and swinging en masse from the ends of branches.

(8) Not-in-territory. Also non-functional, this category simply allowed short term absences from the territory to be scored.

(9) Nest-building. Nests were built by females, beginning in early June each year.

(10) Incubation. Eggs were incubated by females only.

(11) Brooding. Nestlings were brooded by females only.

(12) Feeding Nestlings. This behaviour was performed by both parents. Only time spent in attendance at the nest was scored in this category, and the term "nestlings" referred to nest occupants including fledglings.

(13) Feeding Juveniles. For some weeks after fledging, young magpies solicited food exchange from adults, and the older birds responded by feeding the juveniles.

4.1.4 Statistical analyses of time-activity scores

Data obtained from the time budget study were analysed with parametric analysis of variance (ANOVA) procedures, using the

ANOVA directive of GENSTAT (Rothamsted 1980). After an initial 3-way ANOVA (using behaviour, month, time), each behaviour category was analysed separately with 2-way ANOVA. The scores (amount of time expended in the activity in minutes) were subject to a square-root transformation which restored additivity to the effects of the factor levels. α was set at 0.05.

4.2.0 Results

4.2.1 Number and distribution of territories.

As outlined in section 2.2.3, partial histories were compiled for 30 territories. Each territory was coded by number (see Figure 2.c), and regular checks were made of the numbers and identities of occupants. The territories were found to be uniformly distributed (see section 2.2.3), and averaged 5 Ha. in area.

A total of 62 nests were found in the study area between June 1978 and January 1982: 7 in 1978; 22 in 1979; 26 in 1980; and 7 in 1981. An analysis of nests contents and productivity has been left until Chapter Five.

4.2.2 Annual cycle of activity.

Nest-building commenced in early June each year, and was continued by females throughout June and July. Age Class

Three and Four magpies were occasionally observed to manipulate nest materials at this time, and to follow the nest-building female. Magpies mated from late July and eggs were laid from early August. By the end of August, adults of both sexes could be observed provisioning nestlings. The young magpies began to follow their parents after 6 weeks, and were seen on the ground from early October.

By late December, juveniles were foraging independently and adult singing behaviour was at a minimum. Several attempts to trap birds between December and early March failed, because territory occupants did not respond to the live decoy at these times. This suggested that territory defence was least intense in the summer.

From March, juveniles hatched the previous spring began to make short flights out of the territory, usually to the nearest flock ground or unoccupied area.

Singing intensified from March, and flock birds made frequent attempts to perch in defended areas. All occupants combined in their defence of it, although territorial group composition sometimes changed around this time. Emigration of nonbreeders peaked in August/September (see section 2.2.2)

4.2.3 Inter-territory behavioural interactions.

The timing and amount of territory defence summed for 9 individuals in territories [01], [06] and [08] is shown on Figure 4.a. Examination of the graph revealed that territory defence activities consumed most time in the early morning period and least during the early afternoon. This reflected the inclusion of singing behaviour which was most intense around dawn, before foraging began. Territory defence occupied the greatest proportion of time in the autumn months (March,April,May) consistent with the qualitative report in section 4.2.2.

Defence behaviour was elicited by the proximity of neighbours, and in some instances, was apparently unprovoked. At first territory holders flew directly at the opponents, swooping high into the air before contact was made. Birds frequently defaecated at the height of the swoop, and the snapping sound made by sharply closing beaks could be clearly heard. Then, after landing both groups stood, bunched separately, on the ground and carolled loudly. At this point, disputes either lost intensity or escalated into fierce displays of aggression. In the latter case, frequent bouts of aerial display were followed by the terrestrial 'bill-down' threat. Birds remaining on the ground performed 'wing-trembling' in response to being dived at. Such aggressive encounters were never observed to result in serious physical damage.

231 magpie-hours of time budget observations were collected from 2 group-defended territories ([07] and [09]). Both groups disbanded in October 1978 without reproducing, although

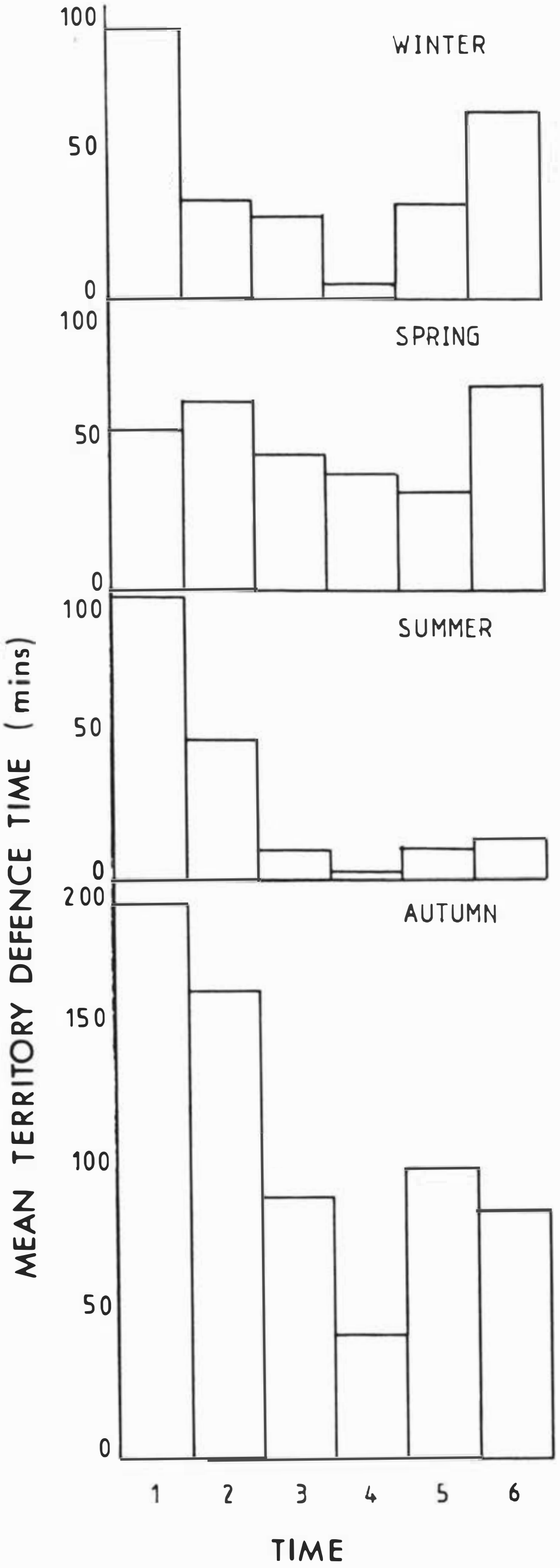


FIGURE 4.a. The distribution of territory defence activity in each day-time period for four seasons.

one adult female returned repeatedly to one place in a tree and sat there for long periods. The time-budgets of these two groups were characterised by frequent aggressive interactions with neighbouring magpies and many absences from the territory. It was judged unlikely that these birds were forced to forage elsewhere since they played for extended periods.

Four of these magpies were colour-banded, and all were resighted in the nonterritorial flock. At the time of trapping none was identified as an adult male, but two (blue-white-green and blue-yellow-red) were later determined to be male from visual inspection in the flock, and one (blue-white-blue) was still in the flock after 20 months. The fourth, (blue-white-yellow) had regained territorial status by 1-7-80, by joining the group occupying the territory adjacent to the location in which it had been trapped. It was impossible to determine whether this animal was a subadult (aged at least 3.5 years) or a female. Male blue-white-green had returned to the trap-site by 14-1-82 and was a member of the same group as BWY. The movements of these birds are sketched on Figure 4.b.

An attempt to establish a new territory was observed in autumn 1980 and described in section 2.2.2. One of the individuals involved had been banded in the flock and its 2 or 3 companions were assumed to be also from the flock.

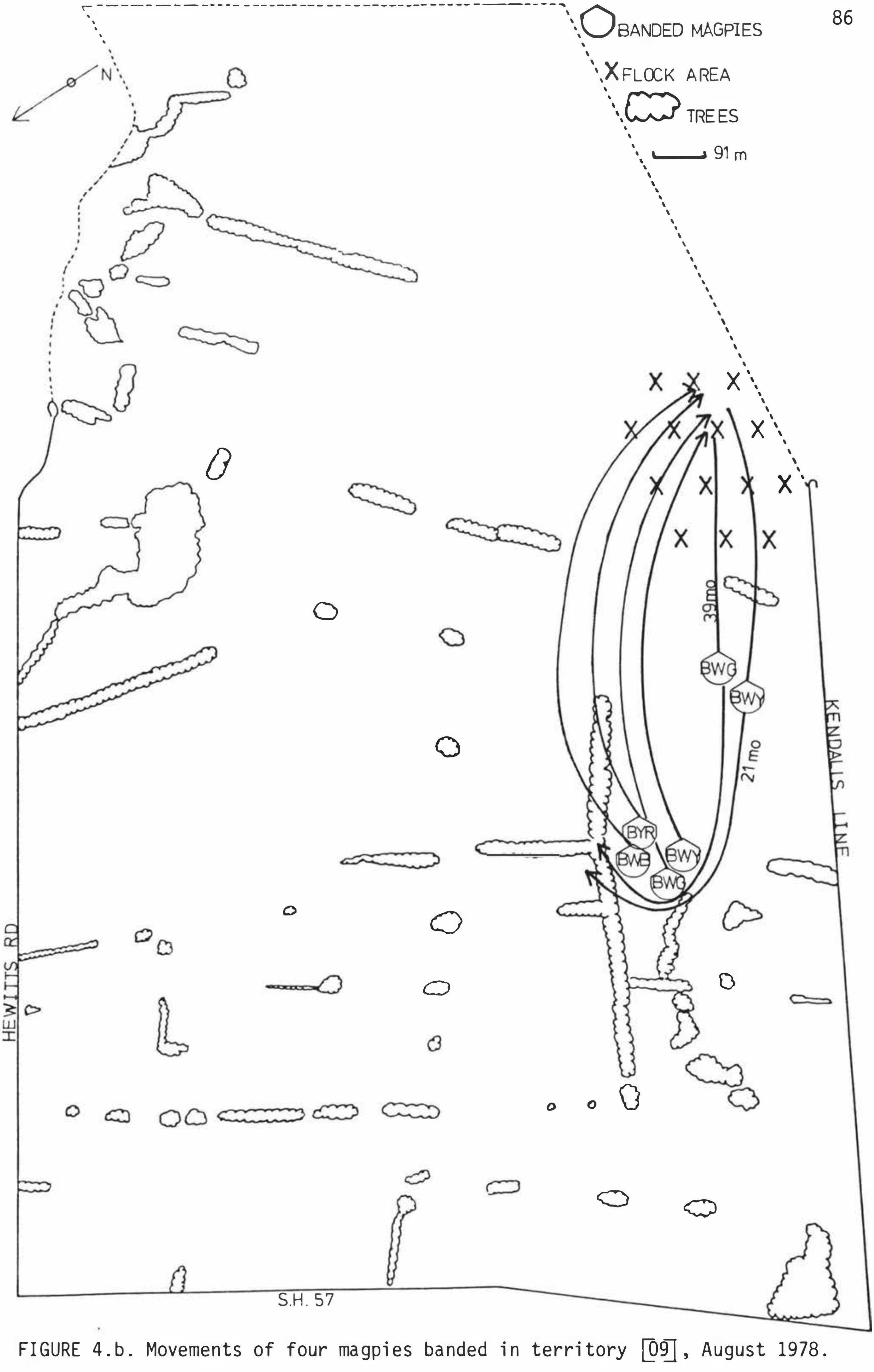


FIGURE 4.b. Movements of four magpies banded in territory [09], August 1978.

One of the two banded males studied in territory [08] (blue-green-red) transferred to the adjacent group in territory [12] during spring 1979. After BGR left the group, one of the subadults in [08] revealed itself to be a male, leaving an adult male complement of 2 in the territory. Territory [12] already contained 2 males, one of which had a malformed and nonfunctional leg. However the cripple dominated blue-green-red throughout 1980, but was gone from the group by March 1981, leaving blue-green-red and another male in residence.

4.2.4 Defence by pairs and groups.

Of the 30 territories surveyed during the study, 9 (30%) were occupied by monogamous adult pairs and the remaining 21 (70%) were defended by groups varying in composition.

Groups originated in two ways. At the end of their first year of life young magpies either remained in their natal territories, or departed to the non-territorial flock. If they remained (as Age Class Four and then subadult members), a family or kin group was formed. Alternatively, small groups of flock birds of unknown relationship attempted to recover territorial status, and if successful were termed non-kin groups. Six territories alternated between occupancy by a monogamous pair and a family group.

4.2.5 Composition of groups.

Group composition varied during the study. The most comprehensive survey was conducted for the January 1980 census, and group composition determined then is summarised on Table 4.a. Of the 18 group-defended territories censused that year, 8 (44%) were occupied by a trio of 2 males and 1 female, and there were 4 (22%) family groups. Mean group size (excluding Age Class Three magpies) was 3.8 in 1980, and 3.7 when averaged over 3 years and 41 records of group occupancy.

4.2.6 Intra-territory relationships.

Behavioural interactions between individuals within territories constituted only 0.1% of the total time-budget, and were infrequently observed at other times. Magpies did not allopreen or perform any other tactile contact behaviour. Group membership may be reinforced by group singing activities, or cooperative defence. Apart from sexual and parental behaviour, social intercourse was limited to play and dominance encounters.

Bouts of play typically occurred in the mid-afternoon. Juveniles interacted with siblings in aerial chases from foraging locations to perching sites, and manipulated sticks and other small objects singly or in company with others. In all, 15 play bouts were watched within territories.

Adults played with their offspring in seemingly mock-tussles on the ground. Usually the younger birds lay in the grass,

TABLE 4.a

Group composition at January 1980 census

Territories	Males	Females	A.C.5	A.C.4	A.C.3	Unclassed
15	1	1	0	1	0	0
18	1	1	0	0	2	1
19	1	1	0	0	2	1
29	1	1	0	1	2	0
02	1	2	0	0	1	0
27	1	-	0	0	0	3
08	2	1	0	1	2	0
17	2	1	0	0	3	0
20	2	1	0	2	0	0
22	2	1	0	1	1	0
23	2	1	0	0	1	0
24	2	1	0	0	0	3
25	2	1	0	0	0	0
30	2	1	0	0	1	0
13	2	2	0	0	2	1
21	2	2	1	1	0	0
26	2	2	0	0	0	0
12	3	2	0	0	3	0

while the adults maintained bill contact with them and hopped from side-to-side over the prone figure. At other times, one magpie walked behind another tugging gently at the first bird's tail and sitting quickly whenever the bird in front turned around.

Adults played together on the ground in a series of mock-fights, or in trees by hanging together from the tips of branches, supported by beak or one leg. Adult play did not seem to be inhibited by hierarchical relationships.

Dominance encounters were observed between adults of the same sex and took the form of low swooping flights at subordinates, who responded by wing-trembling or vocalising in a manner resembling juvenile begging. Birds displaced each other at perches, but without overt signs of aggression. Monogamously paired adults never behaved in this way.

Aggressive interactions among group members intensified from June until September. Females attacked each other, destroyed the nests built by group-mates and flew aggressively at soliciting females (see section 4.2.7). One such exchange was observed between females known to be mother and daughter (see section 6.2.2).

In November 1980, 2 males in [12] persistently attacked a sub adult (Age Class Five) bird in the same territory, who made begging noises and wing-trembled, but remained in the territory. In another incident, when one of two banded males in [02] was shot in 1979, the other male continued to defend the territory with the two resident females until the end of the study.

4.2.7 Sexual behaviour.

In total, 10 copulations were observed during the study. In each case, the mating was initiated by the female participant, who indicated her readiness to mate by perching near her nest and "soliciting". The solicit display (Figure 4.c) involved rapid vertical vibrations of the tail accompanied by wing-trembling. Hens crouched slightly during the display and pointed the beak skywards. Females did not vocalise while displaying and usually solicited in the mid-morning.

After a short interval, a male flew directly to the displaying hen, mounted her and copulated. The encounter was terminated by the male dismounting and flying to another perch. Mated females fluffed out their feathers and, if not interrupted, entered the nest and remained there for several minutes.

Two of the observed matings involved Age Class Four and Five females. Soliciting was performed by a captive-reared magpie at four months of age, and Age Class Three and Four magpies were observed soliciting in the field on several occasions.

On 3 occasions early in the season (mid-June, early July),

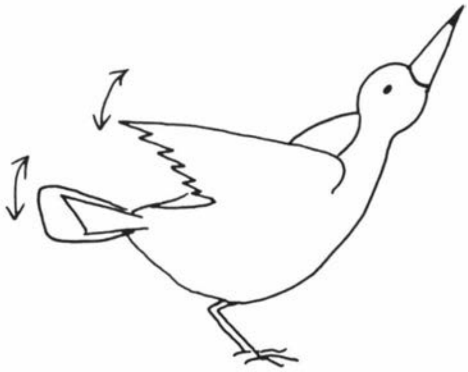


FIGURE 4.c. Pre-mating display by female magpies.

monogamously paired males chased nest-building females into the trees and once, the male-female pair fell from the tree locked in contact.

An opportunity to observe the mating activity of the birds in a group-defended territory occurred in July 1981, when the single female in [28] solicited for 10 minutes near her nest, attracting both males in the territory to the tree. While one male perched near the base of the tree, the other hopped from branch to branch close to the trunk until he was above the female. When he flew onto the hen, the second male immediately flew up to the pair and caused the first male to fly to a lower branch in a flurry of beak-snapping. The female began to solicit again and once again the first male flew to her, and copulated. The second male flew away, followed and then joined by the first.

A description of the mating display by Sicker (1946) was in fact a misidentified play bout.

4.2.8 Cooperative breeding.

In many group-living species of birds, nonbreeders assist breeders at the nest (see section 5.0.0). However, only two instances of helping behaviour during breeding were observed during the study.

In October 1979, the two males resident in [08] each fed the incubating female when she begged. Monogamously paired males never fed a nesting female. Although both males in territory [17] were seen carrying beakfuls of insects in September 1980, only one actually fed the nestlings. The same males remained in close proximity in July 1982, and neither fed the incubating hen although she was audibly begging.

In the second instance, during conditions of food abundance, one female whose own nesting attempt had failed fed the fledged offspring of the other female in the territory (see section 6.2.3).

Age Class Four and Five auxiliaries were never observed to assist with nestlings or juveniles.

From Spring 1978 to spring 1981, 14 breeding events in 6 group-defended territories containing two adult females were monitored. Two females built individual nests in 7 territories, only the single female built a nest in 3 territories and the number of nests was unknown in the remaining 4 territories. Of the 7 twin nest efforts, 3 were reduced to a single nest as the result of fighting between the females. In territory [12] in spring 1979, a subordinate male fed the nestlings of the subordinate female. Subordinate hens delayed laying until the dominant female was incubating her own clutch.

4.2.9 Juvenile and subadult dispersal.

Of the 58 surviving juveniles hatched between spring 1978 and spring 1981 in the 12 regularly censused territories, 51 (88%) emigrated from the territory at the age of one year. The other 7 (12%) remained in the natal territory for one more year. Four of these birds (6% of the total) stayed in their territories as subadults.

As described in section 2.2.2, juvenile dispersal (and hence flock formation) occurred as the next cohort was fledging. Age Class Three magpies began to make short flights away from the natal territory during their first autumn, usually to the nearest flock. The periods of absence extended from minutes to several hours, until finally the birds were no longer resident in the territory. Aggressive incidents involving adults and their Age Class Three offspring during the autumn and winter may have contributed to juvenile dispersal (see section 4.2.6). The proximate stimulus for emigration was unknown, but see Chapter Six.

Although the Age Class Four sample was small, a lower proportion of these birds emigrated from the territories in the following year. Magpies which stayed at home during the first cycle of dispersal experienced (approximately) a 50% likelihood of becoming permanent residents.

4.2.10 Time-Activity Distributions.

Between September 1978 and August 1979, 848 hours of observation yielded almost 2500 magpie-hours of time-activity data from 9 adults in 3 territories. The sampling effort is summarised on Table 4.b.

When activity scores were averaged over all individuals and daytime periods for each month regardless of the sex of individuals, three non-reproductive activities were predominant in the time budget. They were foraging, perching and territorial defence, and their distributions are presented on Figure 4.d. When the reproductive months (August, September, October) are omitted from consideration then foraging occupied between 48% and 63% of a day; perching took 35% to 46% of the day, and territorial defence used 0.5% to 6% of the day. Whenever a decrease in foraging activity was recorded between months, perching behaviour increased. The proportion of time spent foraging decreased steadily through the spring and early summer, but mid-summer foraging levels were higher. Territorial defence levels peaked twice: in October/November (when dependent juveniles were in the territories), and during autumn.

Separate male and female time-activity distributions for the breeding season are presented on Figure 4.e. In August, females (n=3) spent the greatest proportion of their time incubating, and the average proportions of time spent in foraging and perching were reduced to 21% and 9% respectively. In the same month, males (n=6, including 1 non-reproductive female) foraged for 53% of the time, and perched for almost

TABLE 4.b

Summary of sampling effort for territory time budgets in real-time minutes

Territories	Months				Times
	SON	DJF	MAM	JJA	
01	852	889	808	589	T_1
	852	889	808	589	T_2
	852	889	808	589	T_3
	679	914	723	643	T_4
	679	914	723	643	T_5
	679	914	723	643	T_6
06	717	886	684	589	T_1
	717	886	684	589	T_2
	717	886	684	589	T_3
	687	918	714	520	T_4
	687	918	714	520	T_5
	687	918	714	520	T_6
08	583	885	658	470	T_1
	583	885	658	490	T_2
	583	885	568	490	T_3
	574	855	712	510	T_4
	574	855	712	510	T_5
	574	855	712	510	T_6

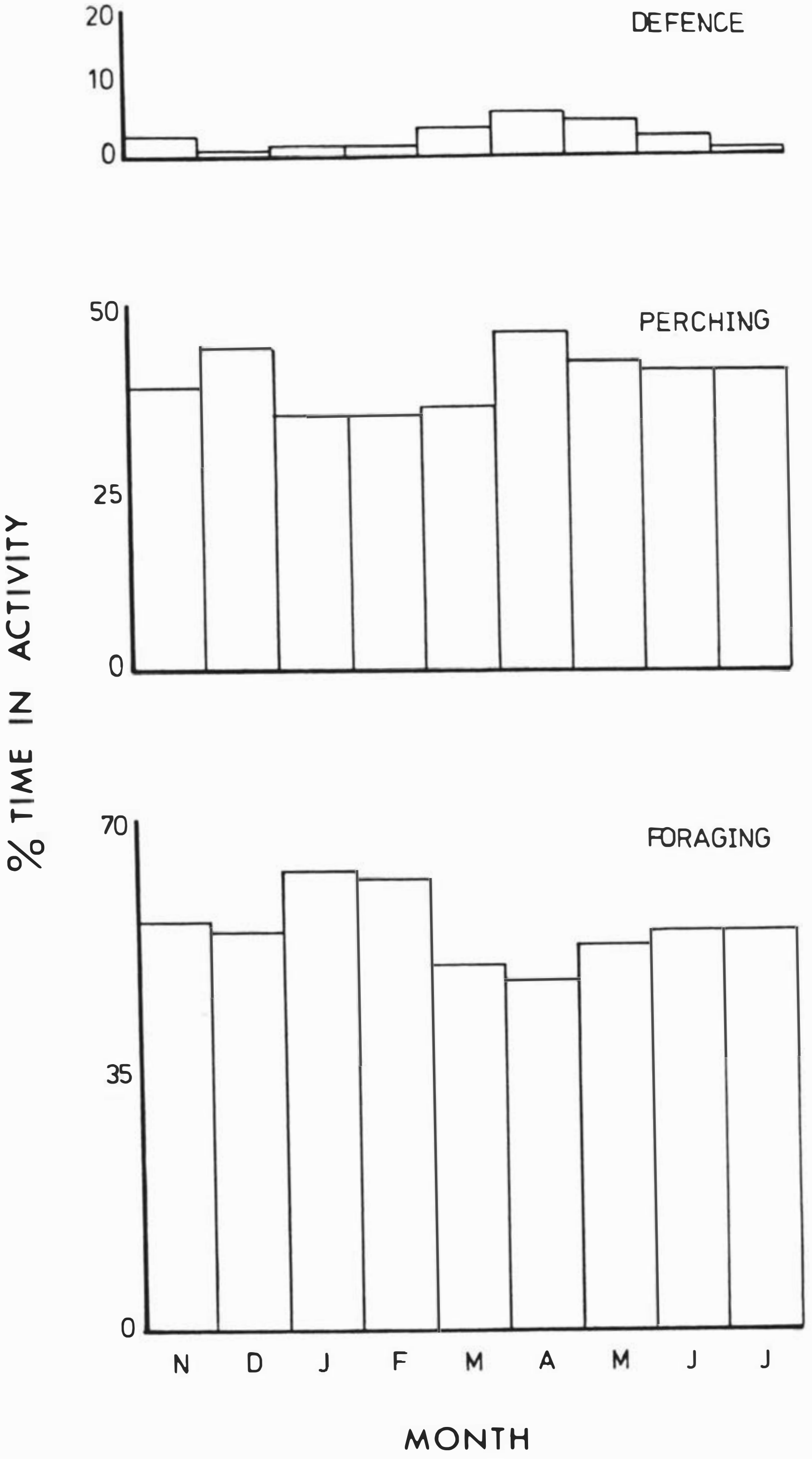


FIGURE 4.d. Percent time expended in three predominant activities from November to July by territorial magpies.

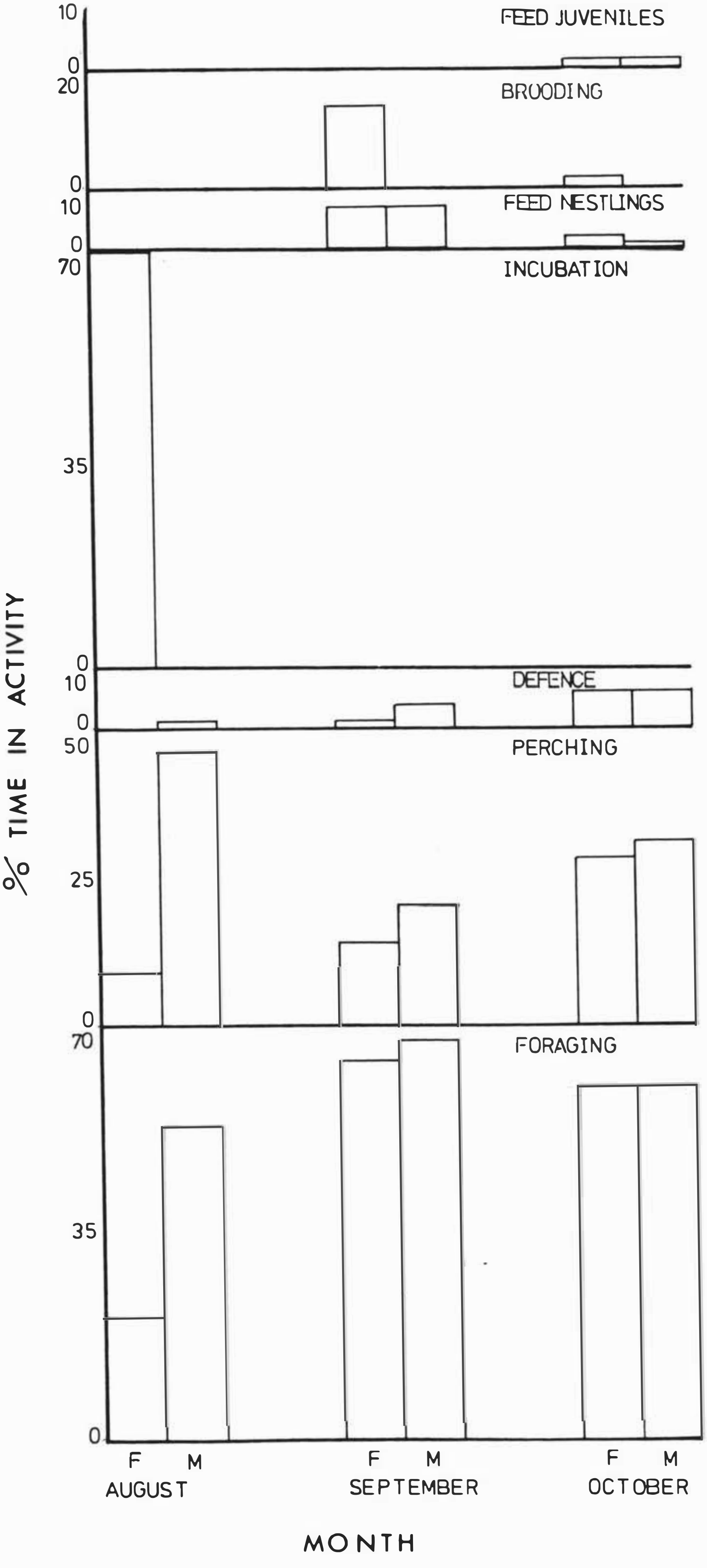


FIGURE 4.e. Male and female magpies time budgets in the breeding season.

all the remainder. Both females and males fed nestlings, and this was reflected in the September time budget. Provisioning nestlings occupied 7% of the day in both cases, and foraging activity accounted for 64% and 67% of the time. Hens spent less time defending the territories than the males, and brooded nestlings for 14% of the day. By October, the female time budget bore more resemblance to the distribution of male activities, except for a reduced contribution to territorial defence and less perching, in favour of brooding behaviour.

Three independent variables; behaviour (13 levels), month (12 levels), and time (6 levels) were examined for their effects on one dependent variable, the amount of time expended by the nine birds under study. After an exploratory 3-way analysis of variance (ANOVA) which tested the seven hypotheses listed on Table 4.c it was found that a square root transformation of the data produced the lowest residual sum of squares (reflecting within-group error), so further analyses were performed on transformed scores only. Examination of Table 4.c revealed that the sum of squares obtained for the behaviour factor was orders of magnitude greater than the values obtained for the other factors and interactions. This was interpreted to be the outcome of uncommon acts such as within-group social interaction, or nest-building, exerting a large influence on the between-group (between-behaviour) variance. In other words, differences in time expenditure between common and uncommon behavioural acts were so great that they may have overshadowed month and time effects on time

TABLE 4.c

Hypothesis	Calculated F	df	Critical F $(\alpha_{(2)} = 0.05)$	Decision
1	7792.718	12	1.75	reject H_o
2	6.879	11	1.79	reject H_o
3	8.012	5	2.21	reject H_o
4	24.872	132	1.22	reject H_o
5	20.299	60	1.32	reject H_o
6	0.563	55	1.35	accept H_o
7	1.821	660	1.00	reject H_o

Hypotheses

1 the time expended was the same for all activities

2 the time expended was the same for all months

3 the time expended was the same for all times of day

4 differences in time expended in each activity were independent of monthly differences

5 differences in time expended in each activity were independent of time of day differences

6 differences in time expended between months were independent of time of day

7 there was no interaction between the effect of activity, month and time of day on time expended

expenditure.

Accordingly, the transformed data were subjected to 2-way ANOVA of month and time factors, for each category of behaviour. A visual examination of the plots of residual versus fitted values and residuals versus normalised residuals served as a check of homoscedasticity (Zar 1974).

The amount of time expended in each of the three predominant classes of activity (foraging, perching, and territorial defence) varied significantly with month and time of day, and was subject to significant interactions between month and time.

A summary of the analysis for foraging activity is presented on Table 4.d. Although all three variance ratios (F values) were significant, the ratio obtained for the time factor was large relative to that obtained from month or the month x time interaction. To visualise the time effect, refer to Figure 4.f where the means of the transformed scores are plotted against time of day for each three-month season. Least time was spent foraging in the early morning and the late afternoon period saw consistently higher foraging levels. The mean amount of time spent foraging in the late afternoon increased in summer.

The analysis of perching behaviour is summarised on Table 4.e. Again, time of day most strongly influenced the distribution

TABLE 4.d

Analysis of variance on time spent foraging
by month and time, for territory magpies

Hypothesis	Calculated F	df	Critical F ($\alpha_{(2)} = 0.05$)	Decision
1*	6.286	11	1.99	reject H_o
2†	47.754	5	2.57	reject H_o
3††	3.433	55	1.43	reject H_o

* the time spent foraging was the same in all months

† the time spent foraging was the same at all times

†† differences between months in the time spent foraging were independent of time of day

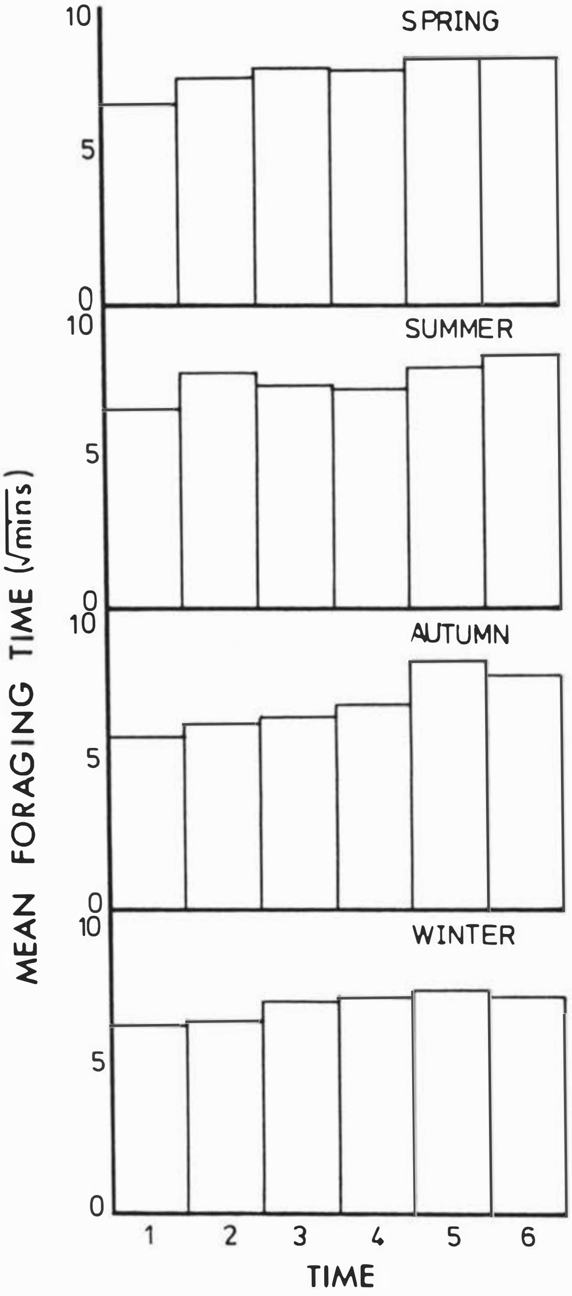


FIGURE 4.f. Seasonal patterns of foraging activity by territorial magpies, over six day-time periods.

TABLE 4.e

Analysis of variance on time spent perching by month and time, for territorial magpies

Hypothesis	Calculated F	df	Critical F ($\alpha_{(2)} = 0.05$)	Decision
1*	8.077	11	1.99	reject H_o
2†	42.654	5	2.57	reject H_o
3††	2.928	55	1.43	reject H_o

* the time spent perching was the same in all months

† the time spent perching was the same at all times of day

†† differences between months in the time spent perching were independent of time of day

of perching activity and the interaction effect seemed small. As demonstrated in Figure 4.g perching behaviour complemented foraging.

The analysis of territorial defence behaviour (Table 4.f) showed that time of day was an important influence, and that month exerted strong pressure on the distribution of this activity. This information was graphed in Figure 4.a above and described in section 4.2.3.

The month x time interactions were determined from the graphs to be quadratic in form, but polynomials expressing each trend were not developed.

By repeatedly plotting the fitted values of individual foraging, perching and territorial defence scores against the residual values (roughly equivalent to amount of error), it was possible to check for obvious individual differences in the amounts of time expended in these activities. The units of measurement for all the graphs were the square root transformations of the original scores in minutes. Foraging behaviour is illustrated on Figures 4.h (1), (2), and (3), and perching behaviour on Figures 4.i (1), (2), and (3). Two females (in territories [06] and [08]) differed in their spring time budgets. In territory [06] the hen spent less time foraging than the cock in August and both male and female exhibited their lowest perching scores in September. The hen in [08] foraged less than the males in August and September,

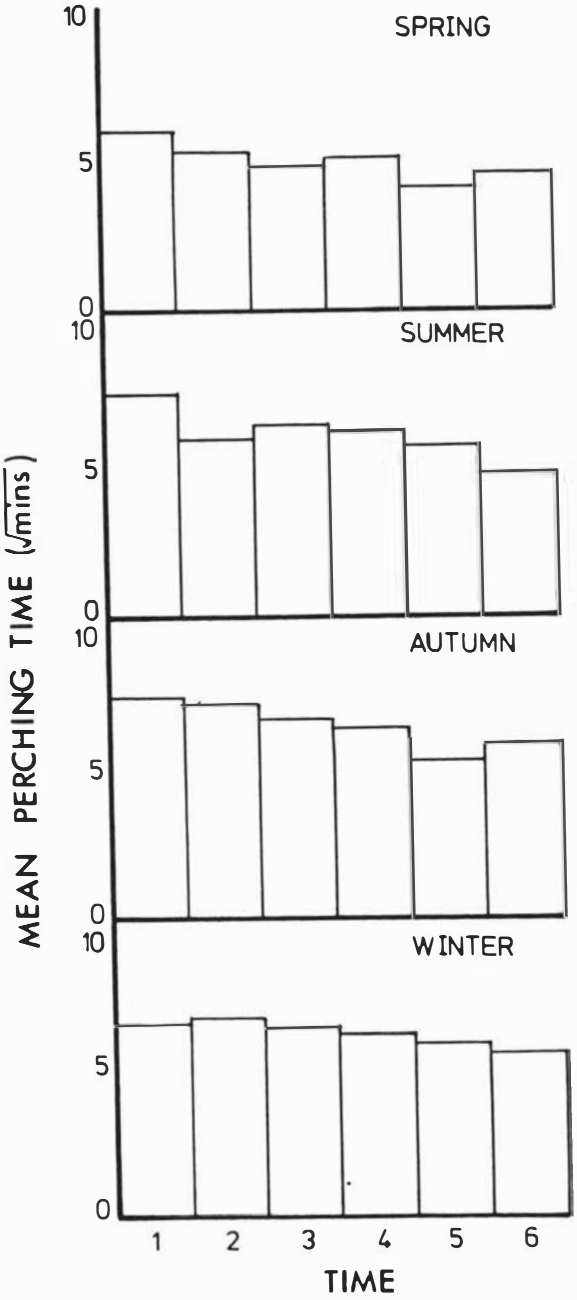


FIGURE 4.g. Seasonal patterns of perching activity, by territorial magpies, over six day-time periods.

TABLE 4.f

Analysis of variance on time spent defending the territory, by month and time

Hypothesis	Calculated F	df	Critical F	Decision
1*	18.097	11	1.99	reject H_o
2†	45.857	5	2.57	reject H_o
3††	4.917	55	1.43	reject H_o

* time spent defending the territory was the same in all months

† time spent defending the territory was the same at all times of day

†† differences in the time spent defending the territory between months were independent of time of day

KEY TO FIGURES 4.h and 4.i

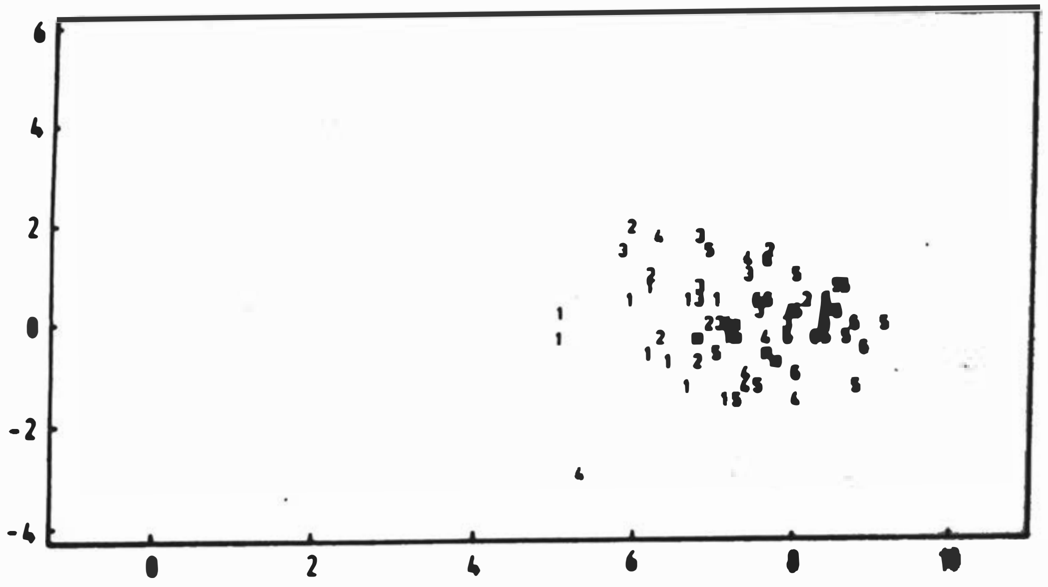
There are two parts to each figure:

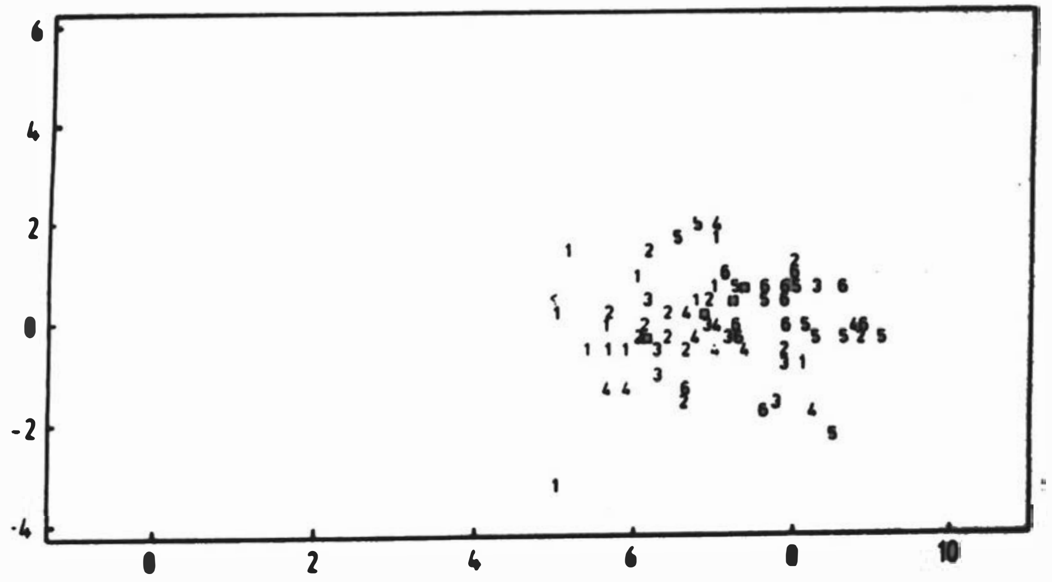
(1) transparency denotes time of day for each score

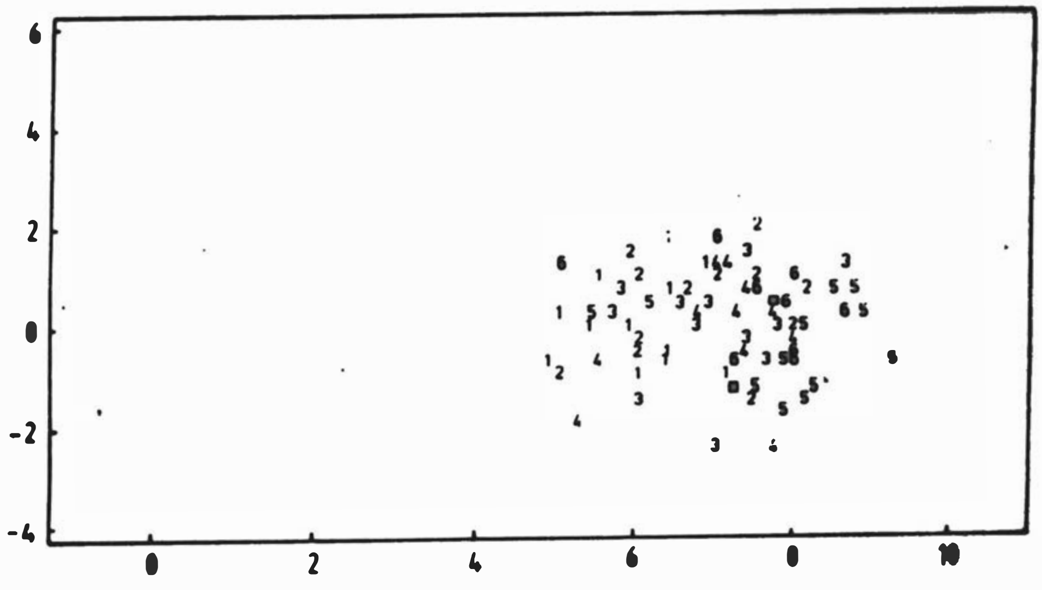
1 - early morning
2 - mid-morning
3 - late morning
4 - early afternoon
5 - mid-afternoon
6 - late afternoon
□ - more than one score

(2) lower copy denotes month for each score

1 - September
2 - October
3 - November
4 - December
5 - January
6 - February
7 - March
8 - April
9 - May
10 - June
11 - July
12 - August
□ - more than one score


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

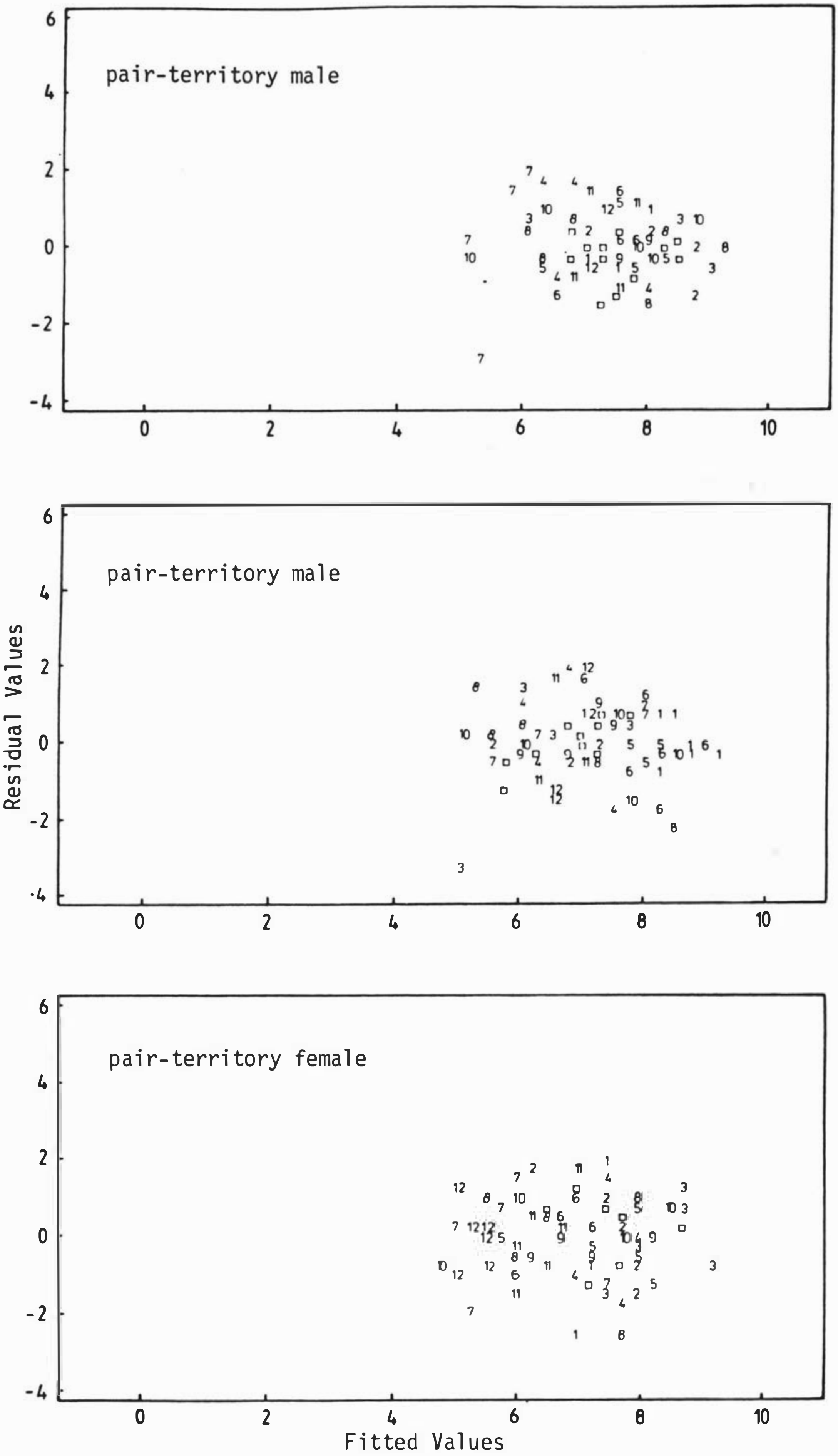
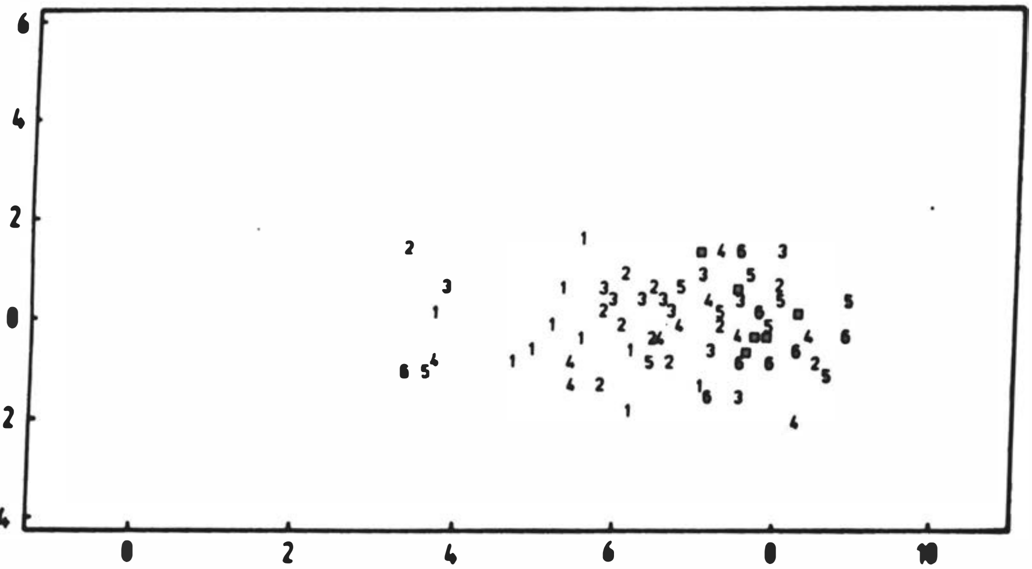
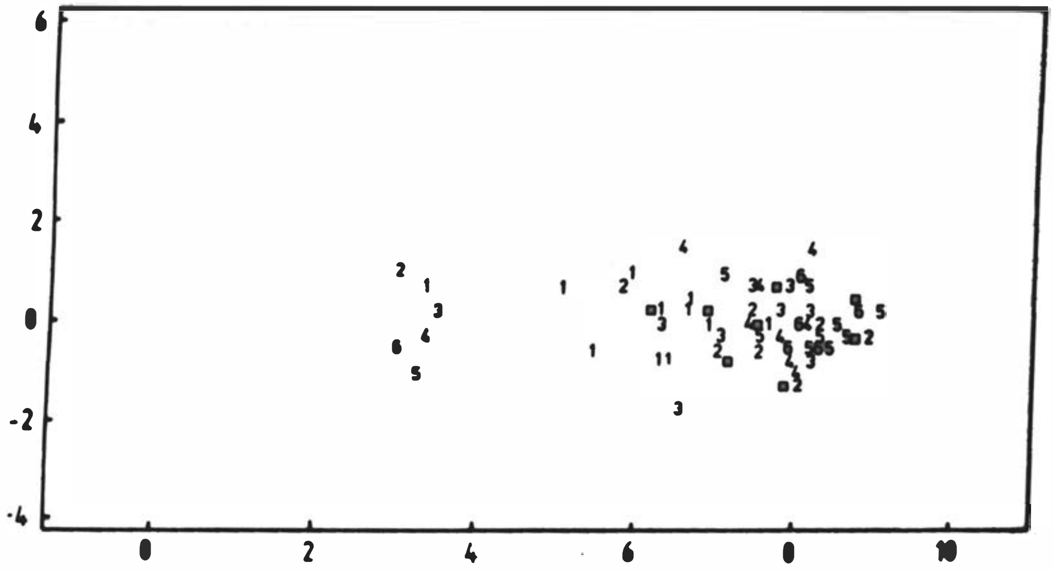
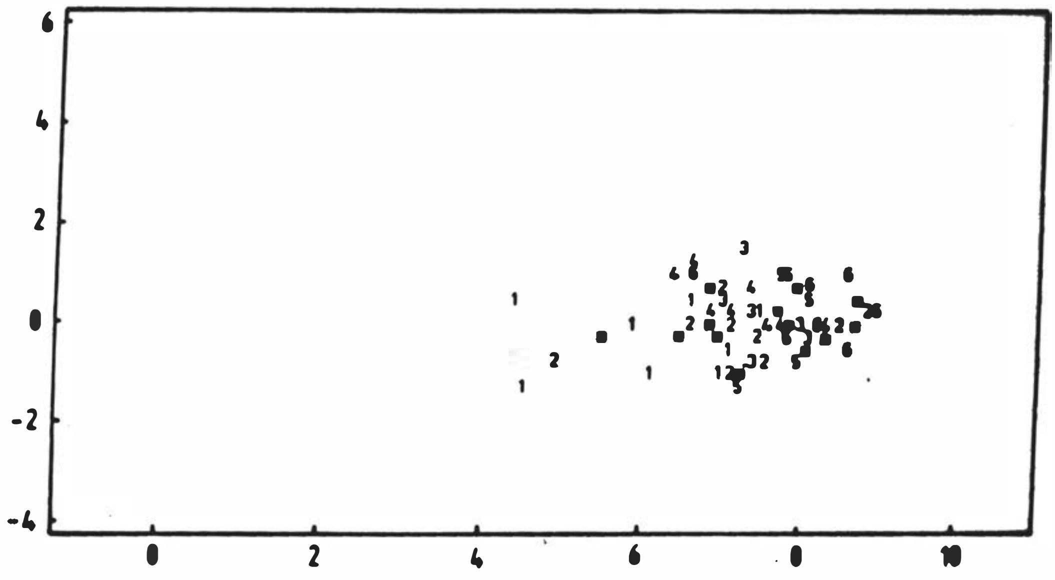


FIGURE 4.h(1). Individual foraging scores.


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

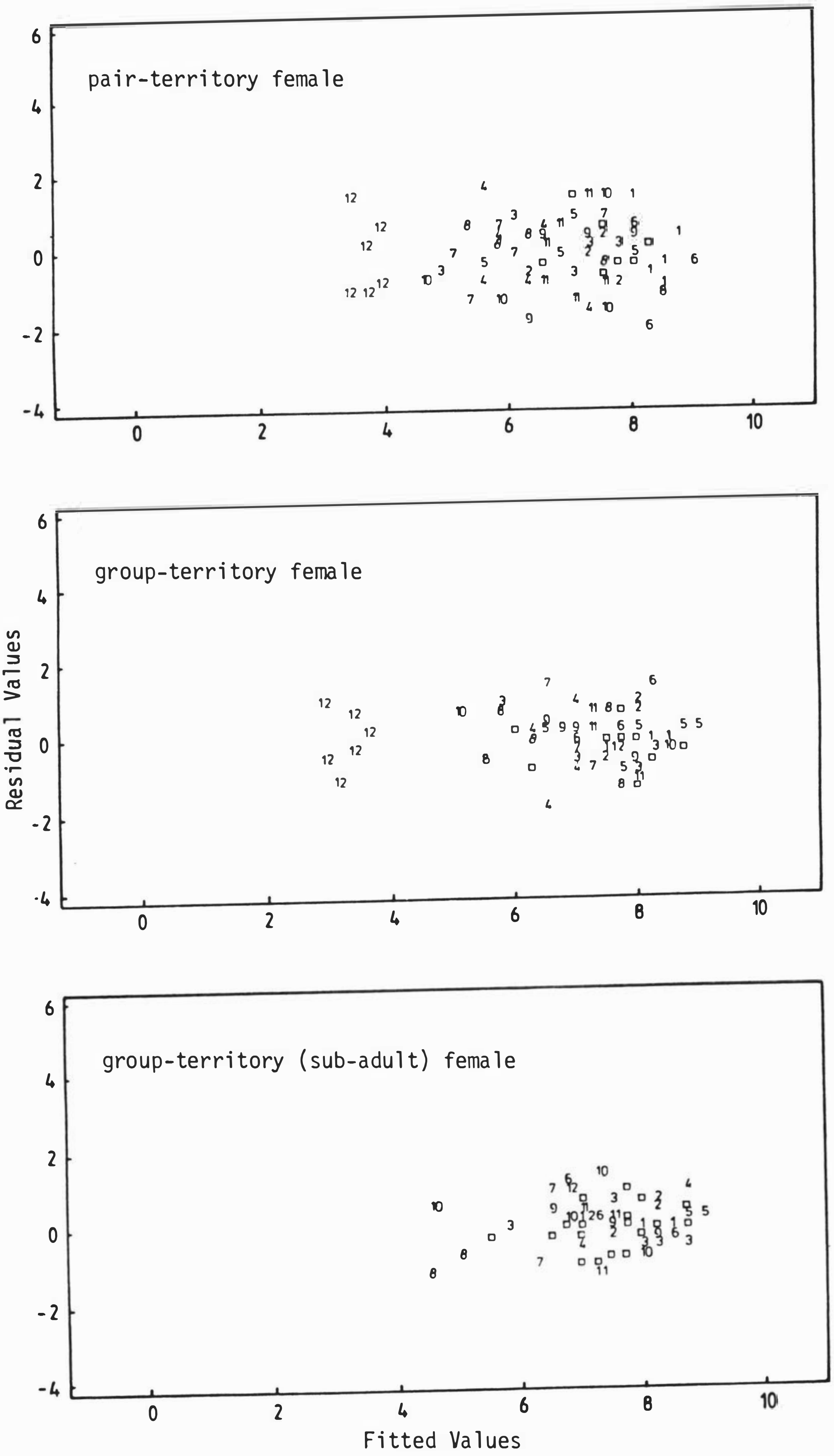
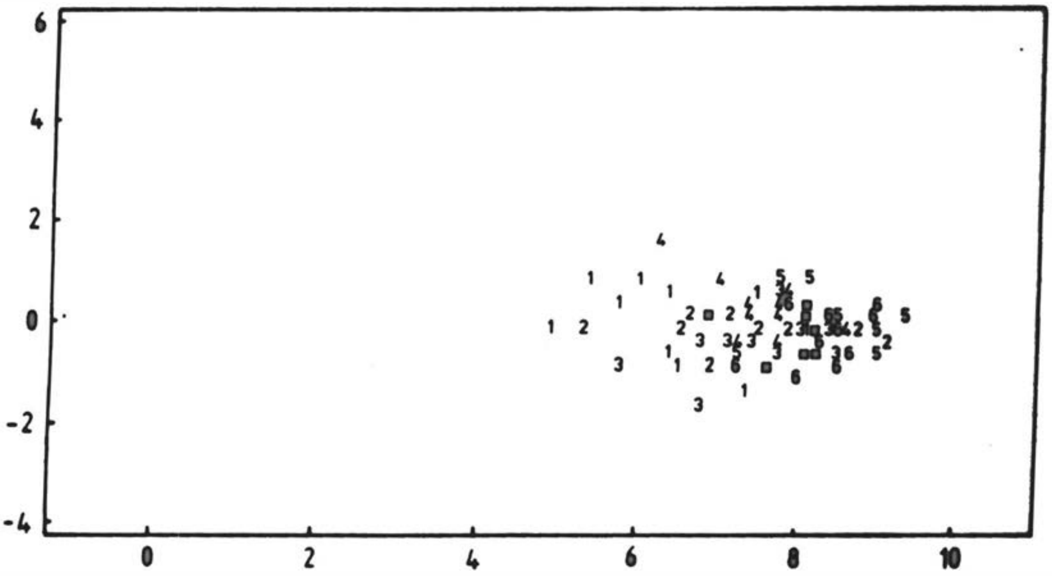
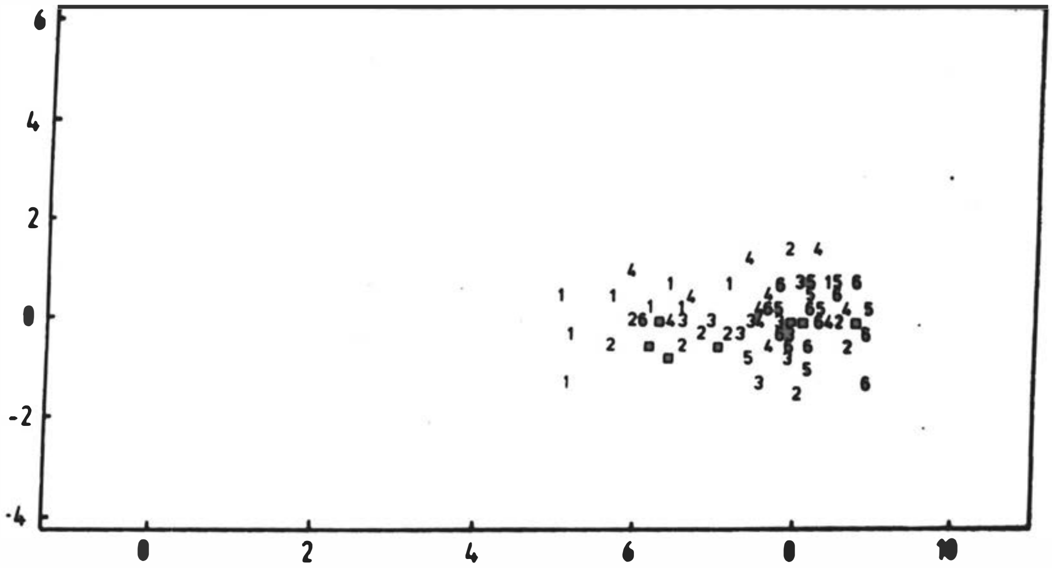
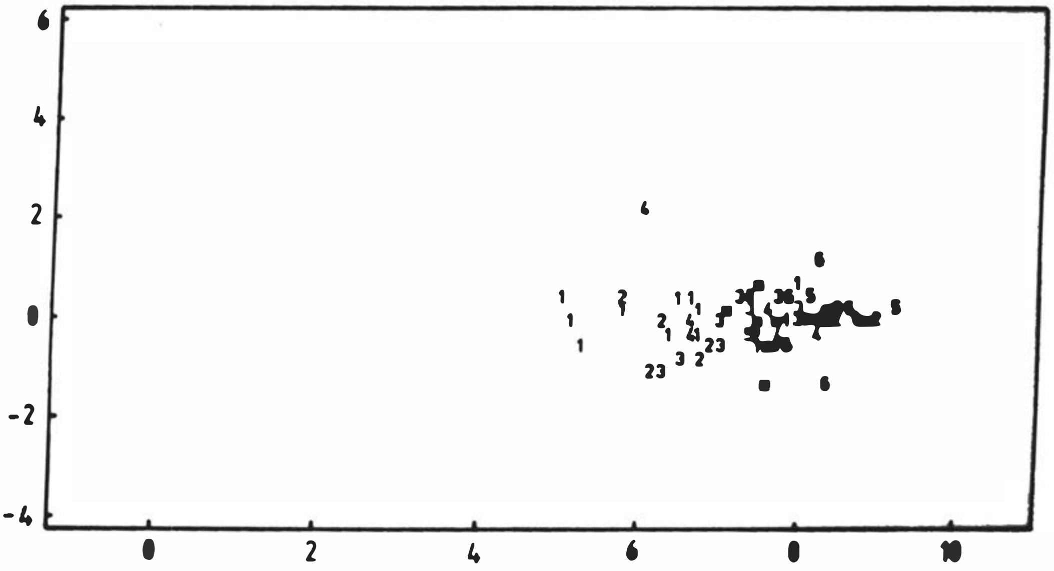


FIGURE 4.h(2). Individual foraging scores continued.


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

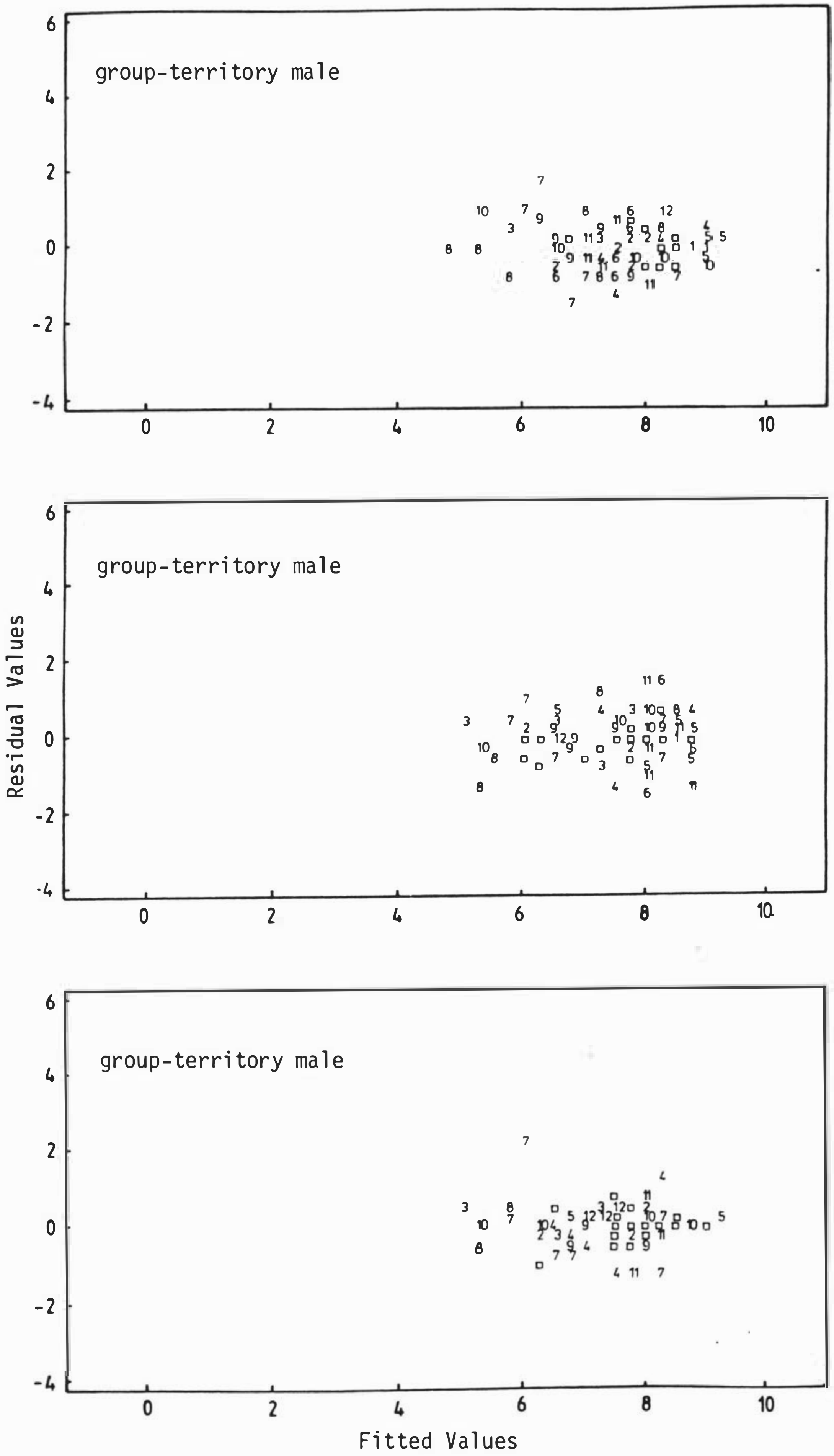
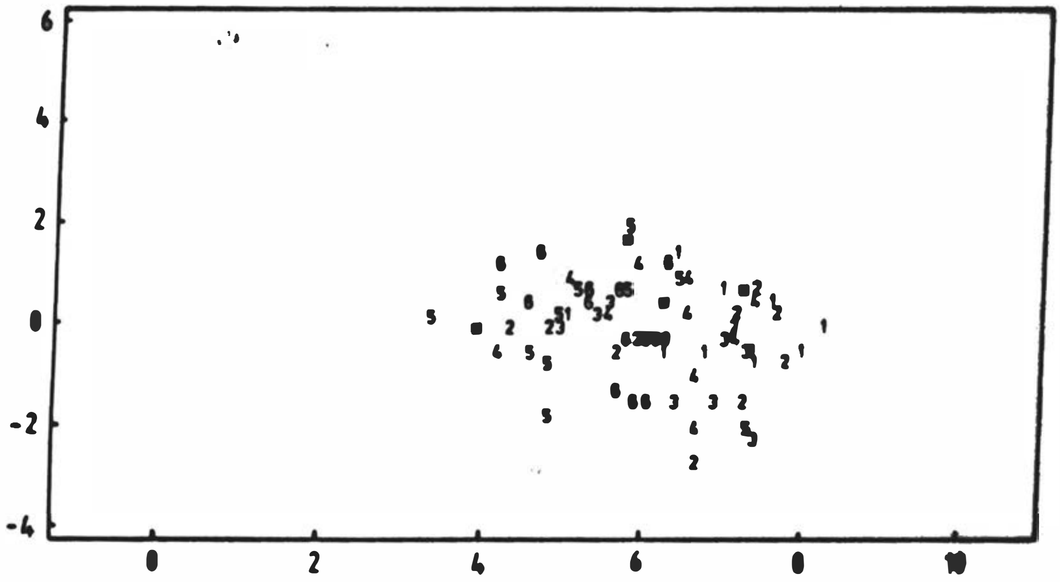
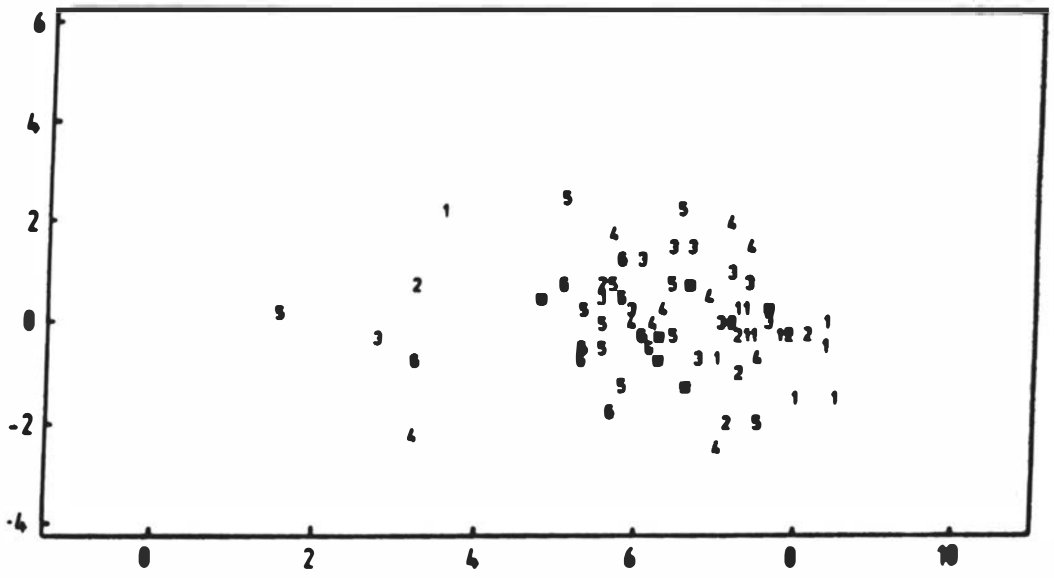
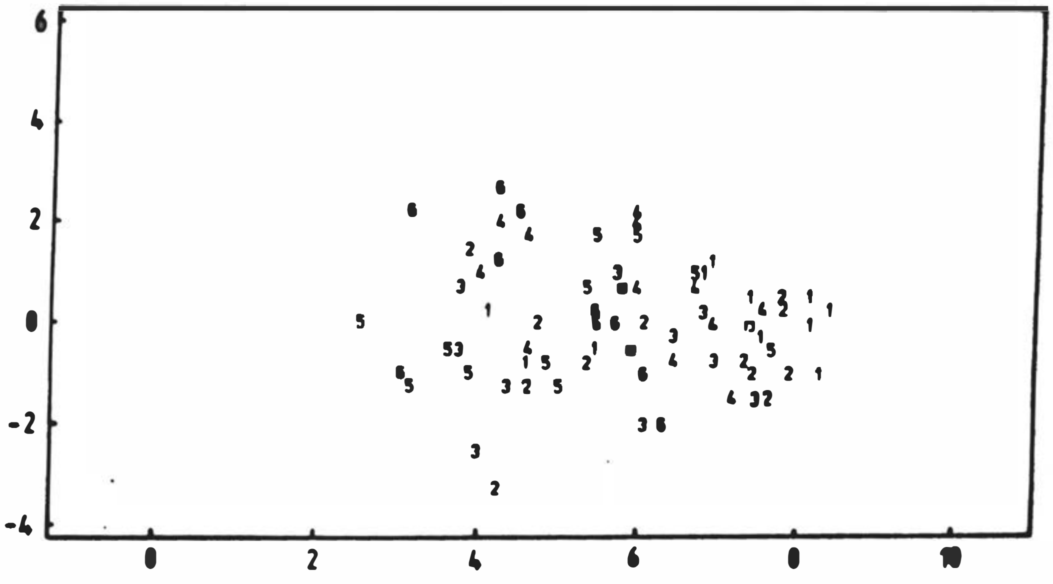


FIGURE 4.h(3). Individual foraging scores continued.


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

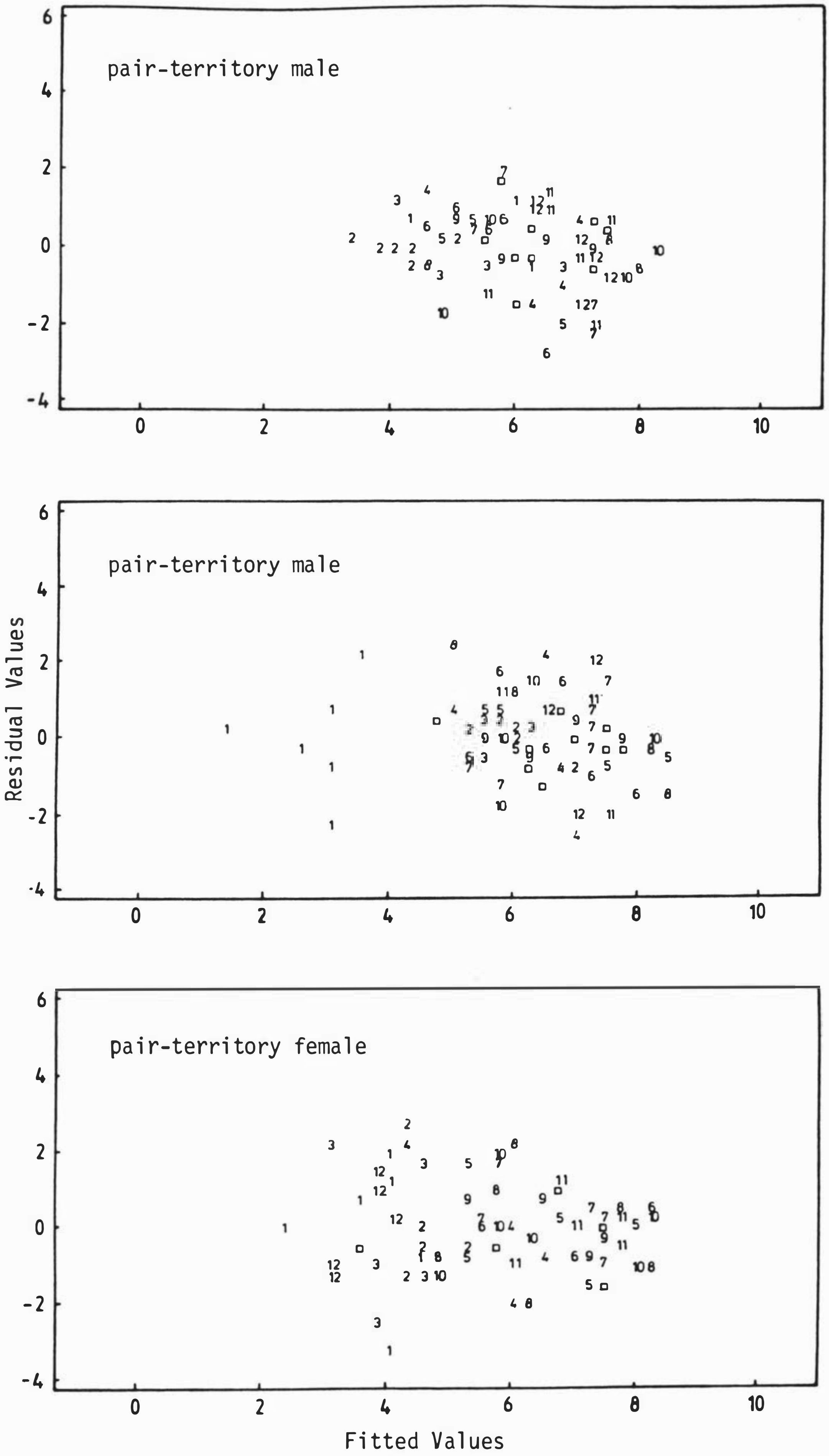
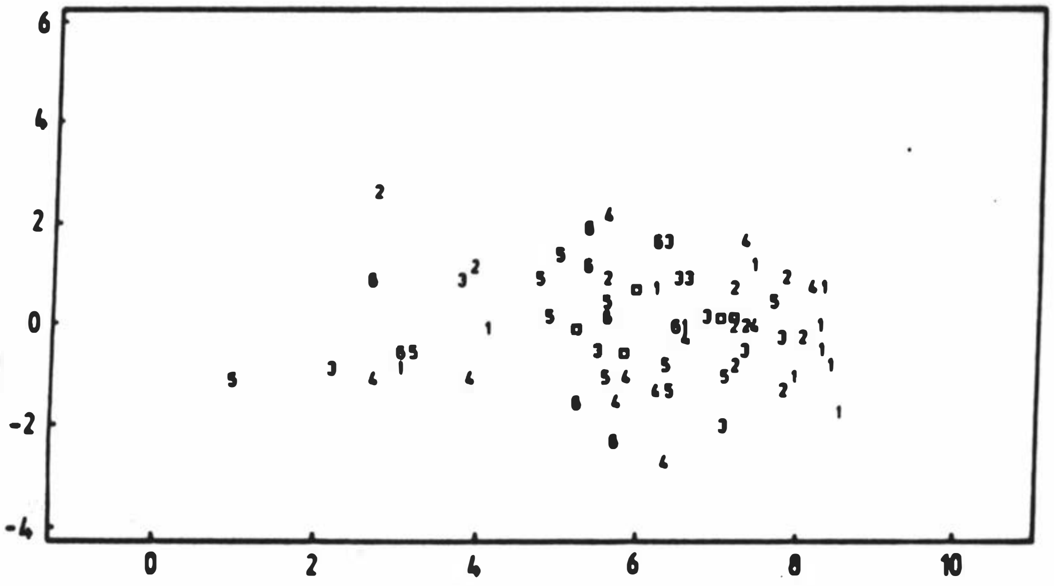
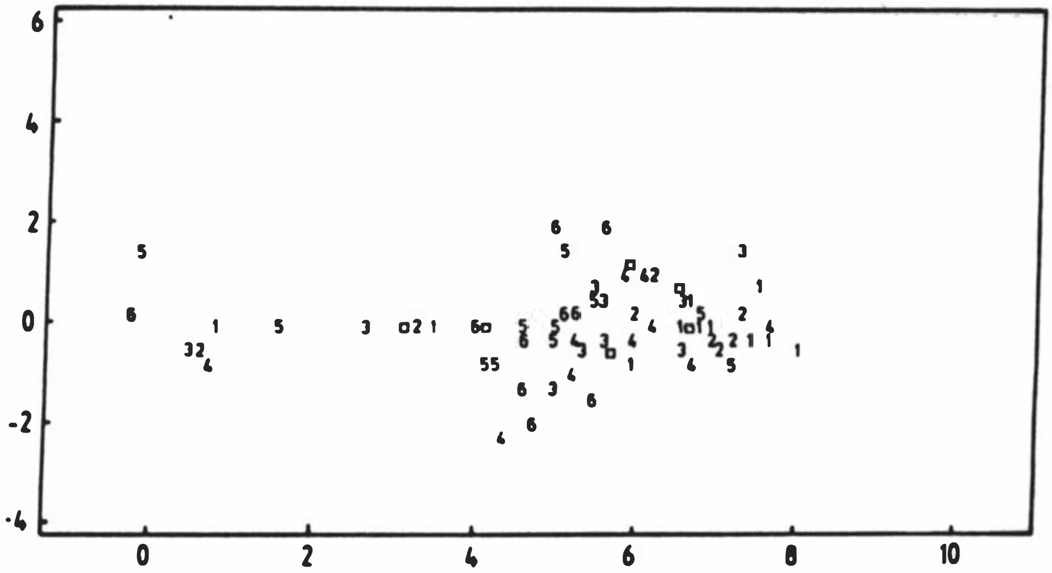
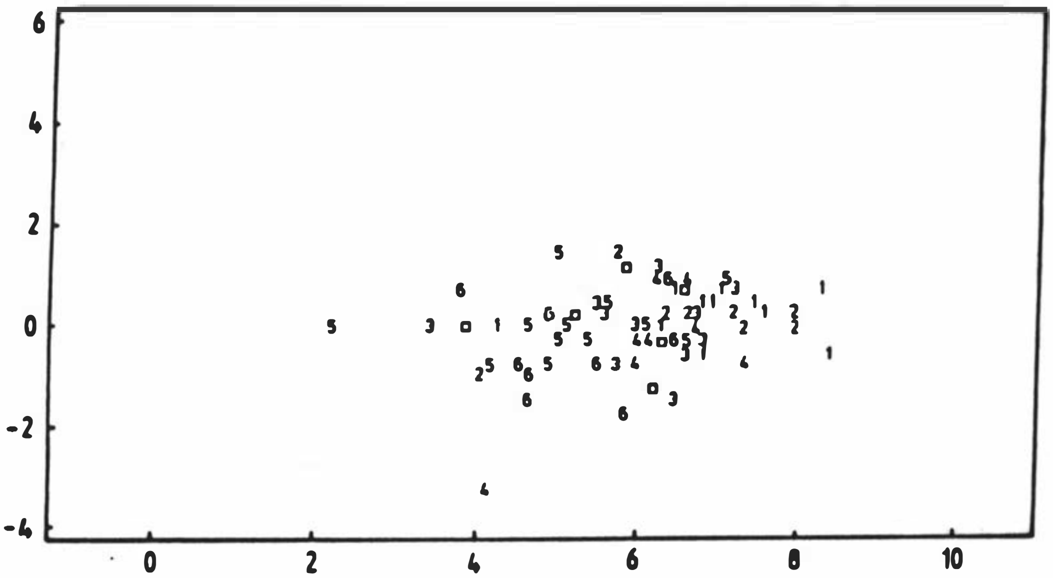


FIGURE 4.i(1). Individual perching scores.


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

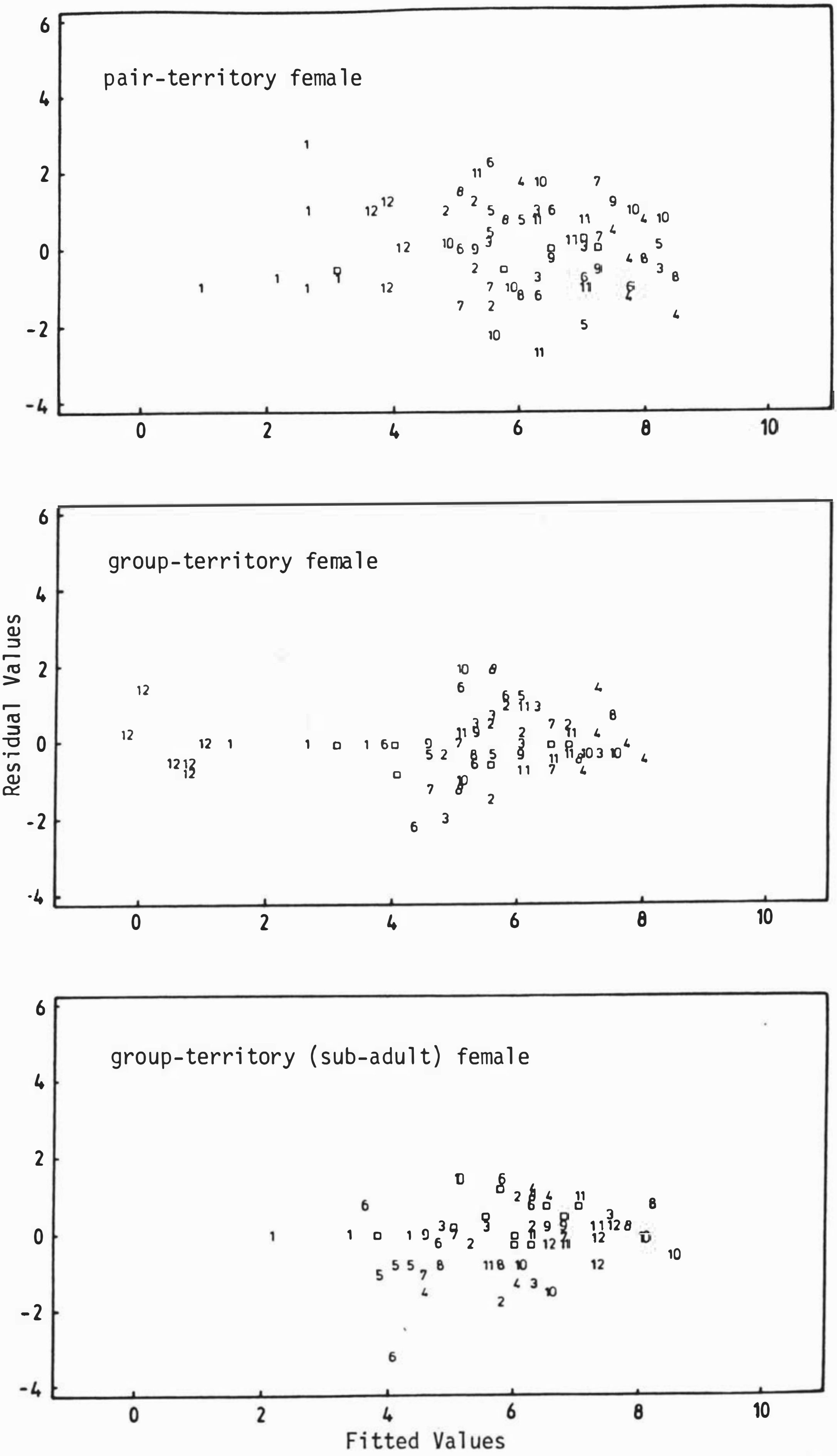
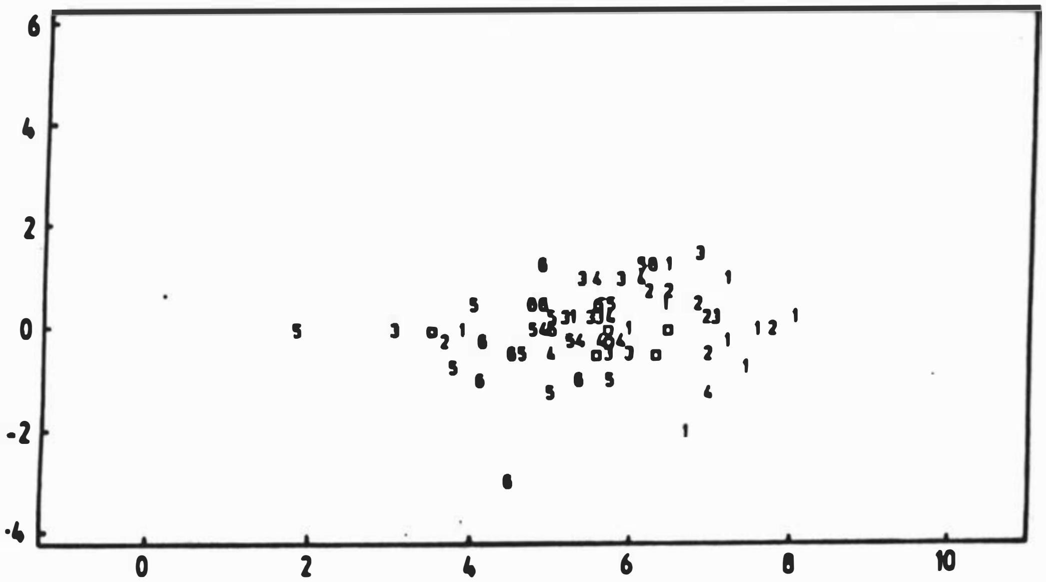
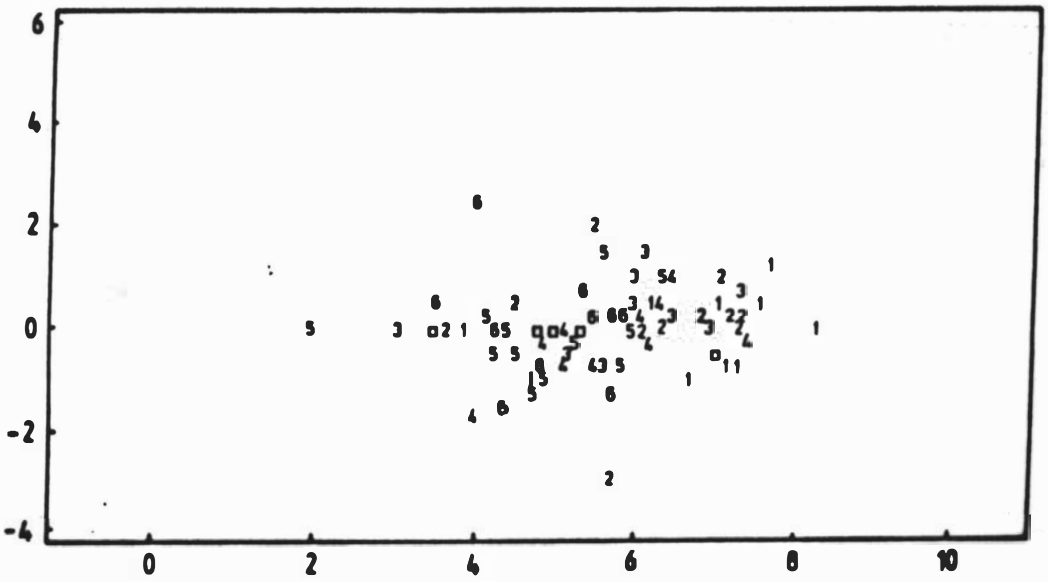
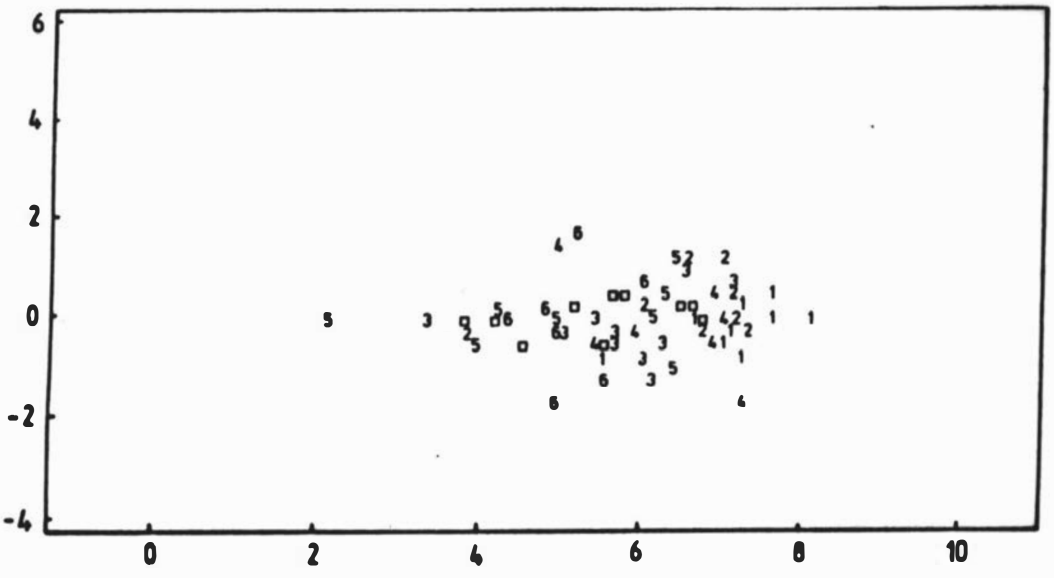


FIGURE 4.i(2). Individual perching scores continued.


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10


6
4
2
0
-2
-4
0
2
4
6
8
10

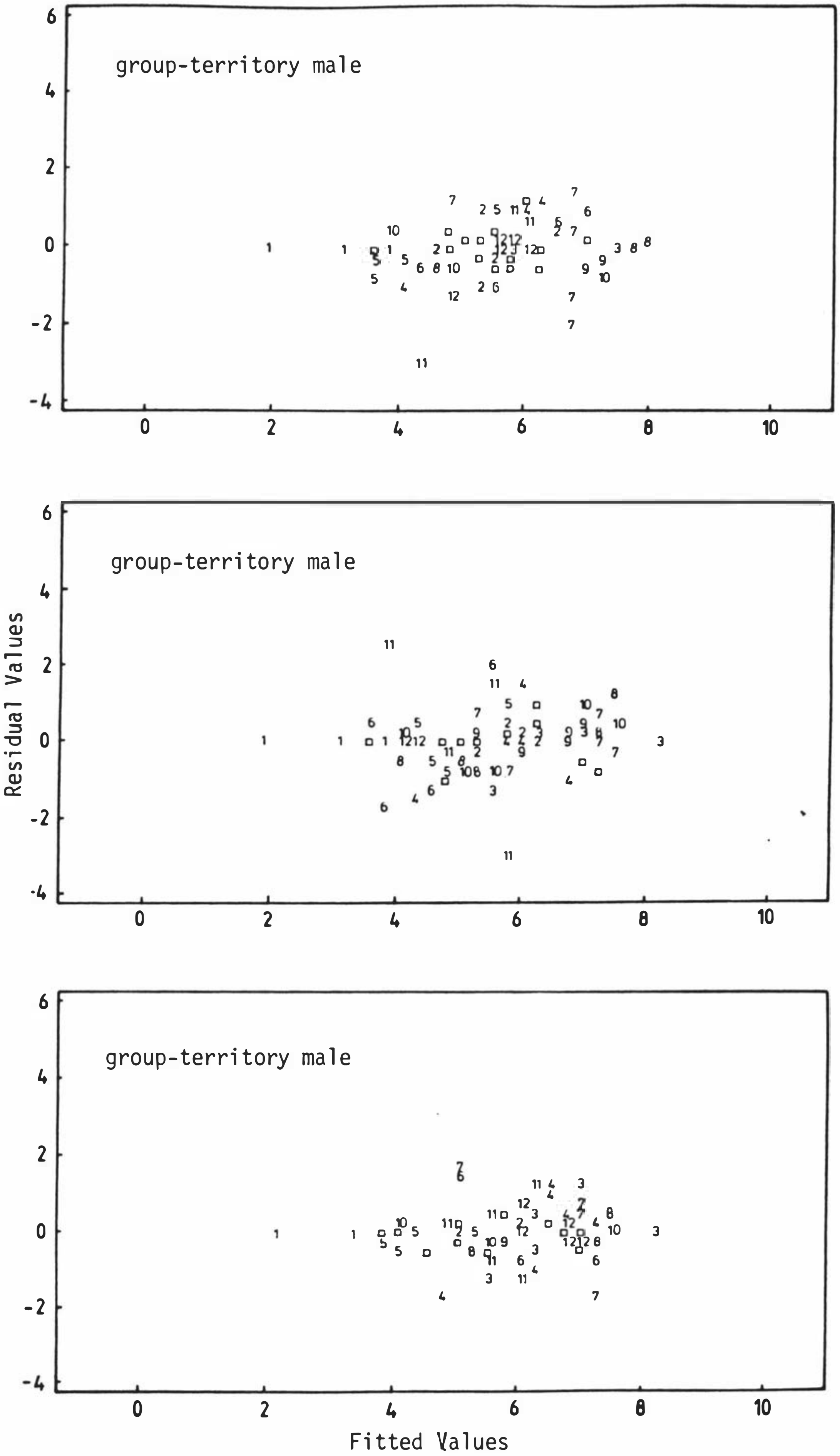


FIGURE 4.i(3). Individual perching scores continued.

and had lower perching scores than the cocks in September. These behavioural differences coincided with incubation and nest-provisioning by the females.

Monthly totals of the time expended in foraging, perching and territory defence by each individual were prepared, and tested for differences between pair- and group-territory males and females using the Mann-Whitney procedure (since the distributions for three individuals were not normal). Group-territory males spent significantly less time perching than pair-males (P=0.0038), and while the group-territory female also perched less than pair-territory females, the difference was not significant. No differences in the amount of time spent foraging were found between pair- and group-territory males or between females.

Significant differences in the time spent defending the territory were found. Group-territory males and the female spent more time defending their territory than the paired males or females did (P=0.002 for males, P=0.019 for females).

The five remaining non-reproductive activities could not be validly analysed using ANOVA since few cells contained values greater than zero. Instead, the non-transformed scores for each individual were plotted for each month and time in a manner analogous to the fitting of response surfaces (Steel and Torrie 1960). Maintenance behaviour was distributed between months and times by individuals without any apparent pattern and was disregarded. These data may have been strongly influenced by the difficulty of observing state changes by perching birds. Antipredator behaviour is plotted on Figure 4.j, within-group social interactions on Figure 4.k, and play on Figure 4.l. Monogamous pairs spent more time in antipredator behaviour than the group-living magpies. Social interactions within social units were confined to July and August, and the two adult males in [08] played in October and November of 1978, when there was no breeding activity in the territory.

Direct parental investment by male magpies began with the hatching of the eggs, from when monogamously-paired and dominant group males began to provide food to the nestlings (see Plate 4.a). A two-way ANOVA on the number of nest visits performed by males and females in each time period failed to detect any influence of sex on this behaviour. In other words, male parents visited the nest as often as the female parents did.

4.3.0 Discussion

Little of the variation in territory tenure described by Carrick (1972) was seen in the Linton population. Three of the 30 territories investigated during the study were short-lived, but the remainder conformed to the description of permanency supplied by Carrick. Neither inner nor outer marginal territories nor mobile groups were detected in the

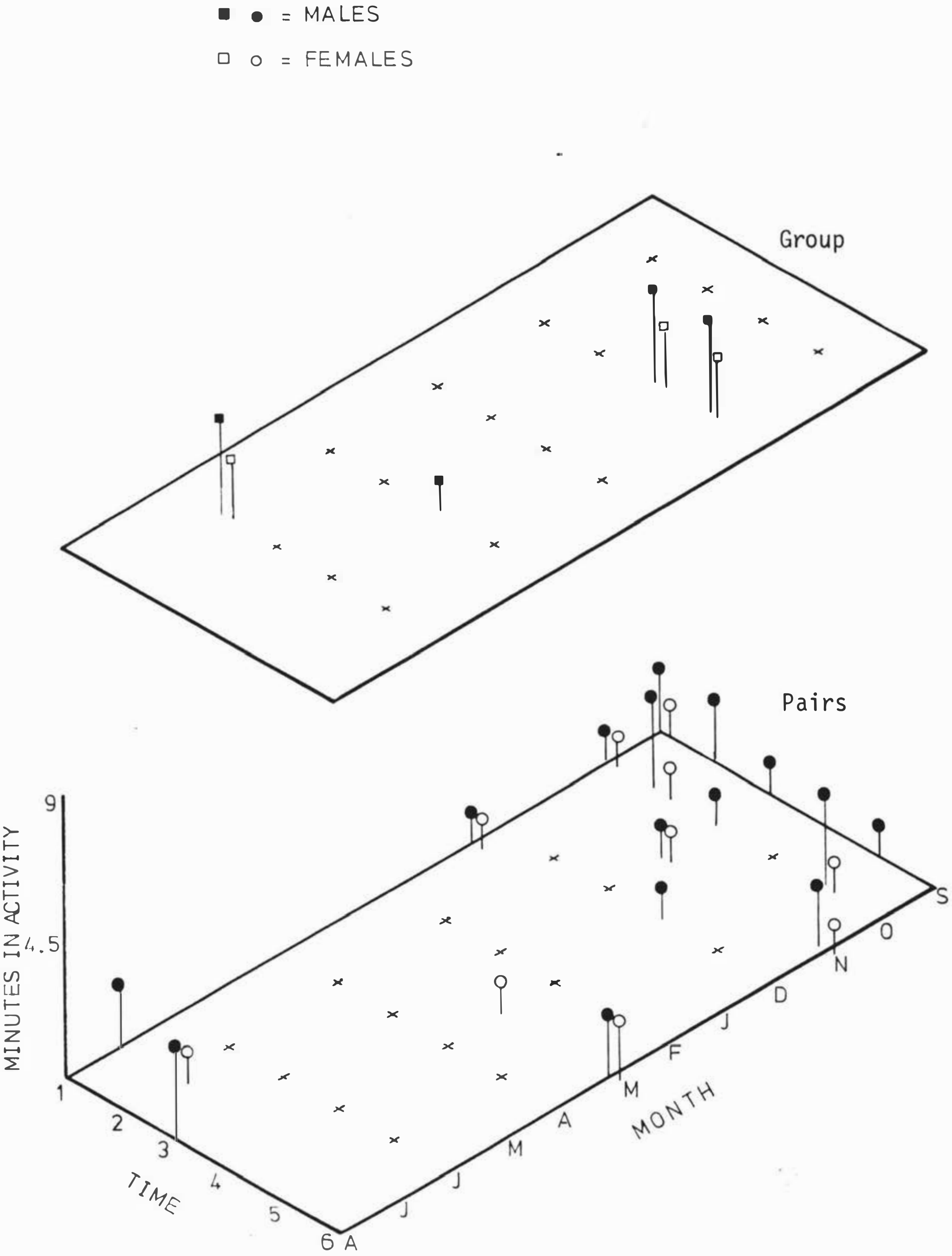


FIGURE 4.j. Distribution of anti-predator behaviour by pair- and group-territory magpies.

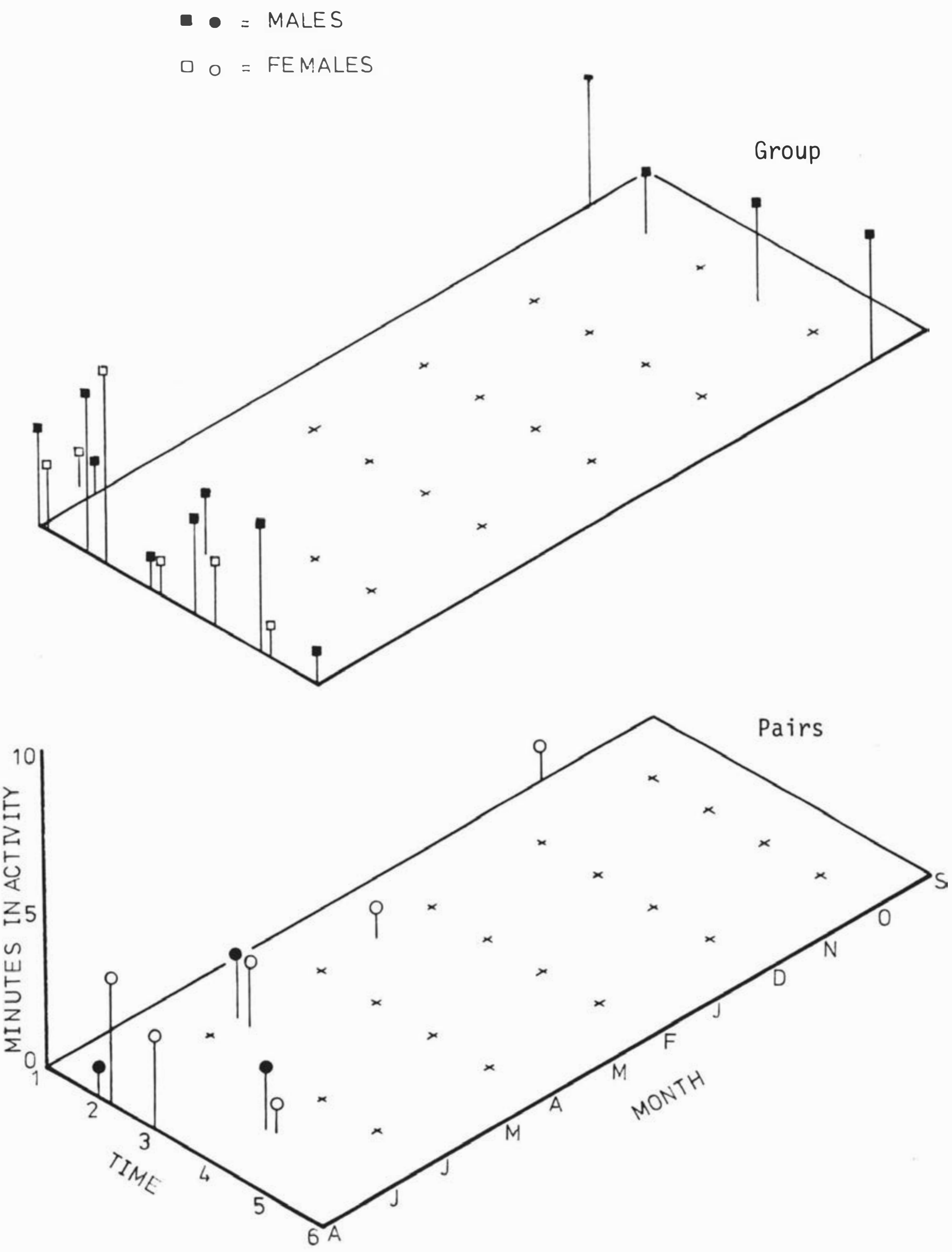


FIGURE 4.k. Distribution of social interactions of pair- and group-territory magpies.

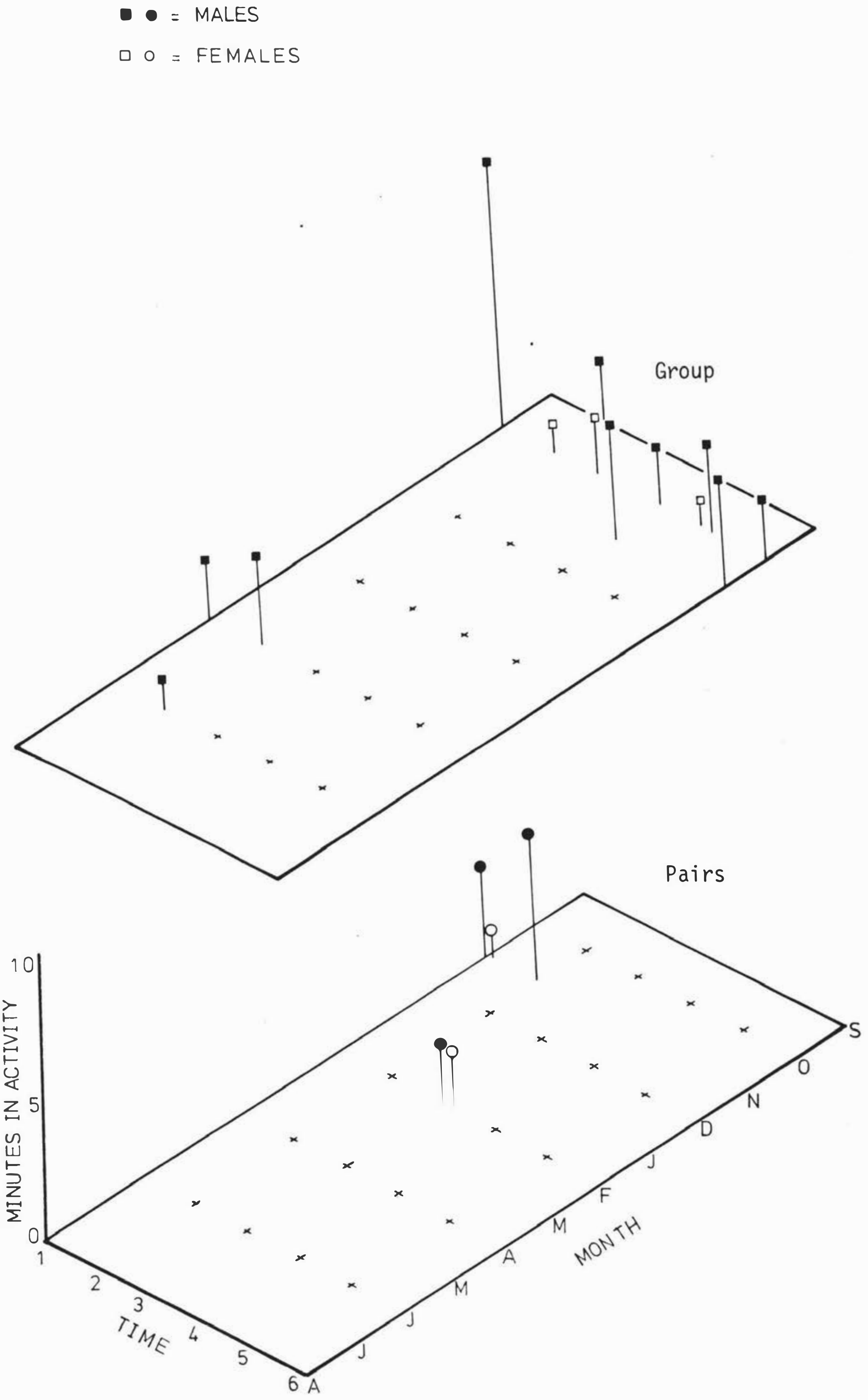


FIGURE 4.1. Distribution of play behaviour by pair- and group-territory magpies.

PLATE 4.a. Male magpie provisions three nestlings.

study area.

Instead, the sedentary phase of the population defended all-purpose and all-year-round territories for several years. The transition between territoriality and nomadism was abrupt by comparison with the Canberra population.

Territorial individuals divided the bulk of their non-reproductive effort between foraging, perching and defending the territory by song and visual display. If a constant level of effort during foraging and constant metabolic requirements are assumed, then variations in the amount of time devoted to foraging reflected changes in the availability of food. Greatest time was expended in foraging during the mid-summer months and it is hypothesized here that prey species type or availability altered at that time. It was anecdotally noted during the study that earthworms were the principal prey in magpie diets at Linton. As soil moisture levels lowered over the summer, so worms may have become more difficult to obtain, entailing a shift to more time-consuming (fewer, harder to find, harder to catch) prey. Although it has previously been argued that food shortages (evidenced by malnutrition) were not experienced by magpies (Carrick 1972), the results of the time-activity investigation described here suggest that food was harder to obtain in the summer at Linton.

As demonstrated on Figure 4.e, foraging behaviour was complemented by perching such that as foraging levels decreased, the amount of time expended in perching increased. The function of the perching behaviour was unknown but rest and surveillance were realistic possibilities. In April for example, relatively large amounts of time were spent in territory defence and perching activity, so that some of the time scored as perching may have functioned in surveillance. The role of rest in the daily time budgets was difficult to assess, since perching time was eroded without apparent penalty during reproduction.

Inactivity patterns in many species were reviewed by Herbers (1981), who modelled the outcomes of a satisficing strategy of foraging in which an animal initiates foraging when it perceives hunger and ceases when it becomes satiated. Such a strategy results in a potential for 'laziness', which she defined as periods of functionless inactivity. It was suggested (Ettinger and King 1980, Herbers 1981) that laziness may not only inhibit energy expenditure and stretch out the intervals between feeding periods, but also provide a buffer time to be utilized when resources are low or metabolic demands high.

Other explanations for long periods of inactivity are that predation pressure has forced animals to lengthen resting times thereby reducing visibility (Biedenweg 1983), or that resting time is subject to physiological constraints (in large mammals, Duncan 1980).

After investigating the relationship between territory size and quality and group size in a Brisbane magpie population, Hughes (et al) (1983) concluded that magpies may be maximising their energy intake relative to the costs of defending a territory. Schoener (1983) recognised two types of energy maximizers; those whose energy intake is limited by the total time available for feeding, and those whose energy intake is limited by food satiation (i.e. processing constraints). Since the magpie time budgets described here include large amounts of inactivity, the former style of energy-maximizing territoriality can be discounted. If magpies are indeed energy-maximizing territory holders, then they must be constrained by food processing requirements. (Interestingly, this is also consistent with a satisficing foraging strategy).

The costs of territory defence for magpies may be expected to relate to intruder pressure, especially from the nomadic phase. If song is both an energetically cheap and effective means of inhibiting intrusion (see for example Wasserman 1982), and if effective physical defense depends on the shortest flight distance from surveillance post to boundary, then magpies should defend approximately circular territories centered on the song and look-out posts. A circular area also has the property of increasing in size with a relatively smaller (square root) increase in perimeter. If intruder pressure increases with perimeter, then the costs of defending such a circular territory decelerate as area increases. Examination of Figure 2.c confirms that the larger territories at Linton were roughly circular in shape.

With this in mind, the effects on feeding time, defence time and optimal territory size of several environmental changes for energy-maximizing territory holders with food processing constraints and costs which are linear or decelerate with area may be summarised. The predictions listed on Table 4.g have been compiled from Schoener (1983). Time spent feeding by energy maximizers cannot be influenced by environmental change, but defence time and optimal territory size may change.

From these model predictions, it might be expected that magpie perching time fluctuated in relation to defence time. Time spent inactive and perching may have operated rather like a bank balance which is drawn on in emergencies. This point is returned to below. The hypothesis that magpies are energy-maximizing territory holders with processing constraints should be tested by experimental manipulations which mimic the environmental changes listed on Table 4.g.

The variety of social units involved in the defence of territories in the Linton study area was documented in section 4.2.4. There were no differences in the sizes of territories defended by pairs and groups. The consequences of territoriality for individual magpies have not been considered before and must vary according to the 'lifestyle' of the bird. The word lifestyle has been used explicitly before (Verbeek

TABLE 4.g

Time budget and territory size changes predicted by Schoener's (1983) model of energy-maximising territory holders with processing constraints

	Feeding time	Defense time	Optimal ty size
Increase in food density	no change	decrease	decrease
Increase in intruder rate	no change	increase or decrease	no change
Increase in food density and increase in intruder rate	no change	increase or decrease	decrease
Increase in intruder rate and decrease in food density	no change	increase	increase

1972, Bekoff and Wells 1981) but without definition, when describing one of several alternative modes of social behaviour within a species or population. Other inter-individual comparisons have focussed on social profiles (for cows, Arnold and Grassia 1983), personality profiles (for eland, Kiley-Worthington 1978), social strategies (for Iberian wolves, Colmenares 1983), and roles (for primates, Gartlan 1968), with a similar aim if not similar meanings. Lifestyle as used in this study refers to an instantaneous subset of response likelihoods to physical and social stimuli, characterising differences between magpies which are more general than individual differences but which are not shared by the whole population.

Four lifestyles were distinguished in the Linton magpie population. They were flocking, monogamous-pair territoriality, non-kin group territorialty and kin-group territoriality. It is stressed here that no information about the genetic relatedness of adult flock birds was available during this study, and non-kin groups were simply inferred. Carrick (1972) described life-histories of individual magpies who experienced several changes of social circumstance without dispersing more than a kilometre from their natal territories, so related adults could be defending territories together.

Differences in lifestyle may be examined on an <u>a postiori</u> basis in two ways. First, individuals may exhibit time-budgets which characterise their lifestyles and the social roles played within them. It was pointed out by Verbeek (1972) that the amount of time expended in various activities depends on differences in lifestyle as well as body size, food availability and physical factors such as ambient temperature. Time budget and social system were linked by Duncan (1980).

The largest inter-individual differences in foraging behaviour reflected the time constraints on two incubating females in territories [06] and [08]. (The hen in territory [01] experienced delays in breeding due to human and storm interference, and eventually renested for the third time in September 1979 after the time budget study was completed). There were no differences between pair and group adults in the total time spent foraging each month and time.

The three group-territory males perched for significantly less time than the two pair-territory males, and there was a suggestion that the group-territory female followed that trend. If perching time was a buffering resource, then territory defence differences would also be expected.

The discovery that the group-territory adults spent significantly more time defending their territory than their pair-territory counterparts supported the hypothesis that perching time represented a pool of inactivity that could be drawn on for territory defense.

Although individuals distributed their antipredator, social and play behaviour differently, no characteristic patterns emerged. All these activities occupied small amounts of time relative to perching. Martin (1982) estimated the energy cost of play at between 2.5 and 10% of the total daily energy budget in mammals and suggested that the incidence of play could provide a sensitive index of prevailing conditions. Although play was absent from the recorded time budget from territory [06], the birds in that territory were observed to play on other occasions. In [08], group members played together in October and November when the pair-territory adults were involved with feeding nestlings and juveniles. Whereas social play in pair-territories like [01] and [06] usually involved adults and their offspring, play in groups took the form of non-aggressive social interactions between all group members and may have had a role in maintaining group cohesion. The development of social and object play in young magpies has been described by Pellis (1981,1981).

Differences in reproductive behaviour characterised the broad differences in parental investment by males and females. No breeding assistance was given by young of previous years but rare incidences of help from adult group-mates were recorded. While the single incidence of female aid may have been a case of misdirected parental care (similar to that observed in Darwin's finches by Price _et al_ (1983)), the involvement of two males with an incubating hen may reflect uncertainty of paternity. Joste _et al_ (1982) found a correlation between the amount of parental care and confidence of paternity for a trio of acorn woodpeckers.

The time budget study demonstrated that there were lifestyle differences in perching and defence activities, such that the group-territory birds under observation incurred a higher defence cost which reduced inactivity. As well, perimeter-dependent costs of defending a circle decrease as the area increases so that the defence effort per individual magpie may decrease with an increase in the size of the territory. Initial resistance at the perimeter of a defended area may only be overcome by the cooperative efforts of a group of birds. Group territoriality seemed to be a mechanism for attaining territorial status and eventually a 'favourable' time budget by individual magpies. Once established, group individuals compete amongst themselves for reproductive opportunities.

The ultimate feature which distinguishes lifestyle differences is reproduction. The alternative approach to comprehending the consequences of individual differences in lifestyle is to investigate the reproductive output of birds in relation to their social behaviour. This problem is addressed in Chapter Five.

CHAPTER FIVE

Reproduction in the Linton Population

5.0.0 Introduction

The problem of reconciling individual and group interests is not unique to magpies. Zahavi (1976) wrote, "The life of an individual group-breeding Babbler is governed by two opposing demands; it must collaborate with its group members in order to survive, and on the other hand compete with other individuals in the group to increase its own breeding success." Emlen (1982) acknowledged that social competition exists in any structured social unit, and argued that each participant should adopt behavioural tactics which will maximize its inclusive fitness. Patterns of interaction between individuals may be ranked on a continuum from selfish to altruistic behaviour (Vehrencamp 1979), with a corresponding decrease in the importance of individual selection.

Classically, the effectiveness of a behavioural strategy has been measured as the rate at which the strategists genes are propagated relative to the genes of other individuals in the population; its individual fitness (Vehrencamp 1979). In practice, individual fitness is measured as lifetime reproductive success (Brown and Brown 1981), and animals are viewed as behaving selfishly to maximise this quantity

(Dawkins 1976).

However, cooperative social behaviour can result in a reduction of individual fitness (or lifetime reproductive success) through altruism (Rodman 1981). Altruism refers to behaviour which benefits another individual (the recipient) at a cost to the performer (the donor), (Hamilton 1963), and may occur when there is a high likelihood that the recipient shares the determining genes with the donor, or there is a high likelihood of later reciprocation, or when ecological constraints favour group living and the behaviour promotes group cohesion (Emlen 1981).

Altruism towards relatives may have evolved through kin selection (Hamilton 1963, West Eberhard 1975, Michod 1981), operating to maximize an individual's inclusive fitness. Inclusive fitness is the sum of an individual's fitness and the additional fitness of relatives devalued by the probability that the relatives possess the same genes (Vehrencamp 1979). Helping with reproduction by non-breeding group members has been regarded as a test case of kin selection (Brown 1974,1983), and a wealth of studies describing cooperative breeding in birds have been published (reviewed in Brown (1974) and Oring (1982)).

Species which exhibit cooperative breeding typically suffer severe habitat, territory or nest-site limitations (Emlen 1978), and have in common the following demographic features:

low fecundity, deferred maturity, high survival and low dispersal (Brown 1974). Helpers are usually recruited via retention of offspring, as in the Florida scrub jay (Stallcup and Woolfenden 1978), the yellow-billed shrike (Grimes 1980) and the Northwestern crow (Verbeek and Butler 1981). In fact, it has been postulated that cooperative breeding needs conditions of high rate of juvenile recruitment relative to adult mortality for its evolution (Ricklefs 1975).

However satisfying the demonstration that altruists are related to the recipients of their aid, other explanations of the evolution of cooperative breeding are emerging. Despite evidence that aid is apportioned relative to the degree of genetic relatedness in some species (bell miners, Clarke (1984); brown hyenas, Owens and Owens (1984); vampire bats, Wilkinson (1984)), modelling studies have shown that altruism may spread nonpreferentially among kin (Weigel 1981, Schulman and Rubenstein 1983). Armitage (1982) found that familiarity was more important in shaping marmot social relationships, and Mumme et al (1983) observed sisters destroying each others eggs in the acorn woodpecker. Helping behaviour was considered selfish by Woolfenden and Fitzpatrick (1978), Stallcup and Woolfenden (1978), Ligon (1981, 1983), Ligon and Ligon (1983) because helpers may receive direct benefits in the form of extended parental care, improved survival, or opportunities to inherit space for breeding (Rowley 1981).

Although frequently cited as cooperative breeders (Crook 1965, Rowley 1976, Dow 1980, Koenig and Pitelka 1981), magpies did not help at the nest in the Linton population (see section 4.2.8). In a review of intraspecific variations in parental care and mating systems, Lott (1984) wrongly identified magpies as alternately territorial or colonial. While it is true that some magpies shared group-defended territories and others were nonterritorial, the evolutionary significance of each magpie lifestyle has not yet been discovered. Indeed, "relatively little consideration has been given to the effects of group living on individual reproductive success " (Stacey 1982).

This chapter investigates the reproductive success of magpies in different lifestyles ("pursuing different social strategies" Vehrencamp 1979), and examines the role of nonbreeding group members in Linton territories.

5.1.0 Methods

5.1.1 Searching for nests.

Breeding hens began to construct their nests in early June each year. The nests were located by direct observation of building behaviour, or by following the bold approaches of adults as they provisioned nestlings. In contrast, subordinate hens in group-defended territories nested cryptically, necessitating careful surveillance.

5.1.2 Examination of nest contents.

Whenever possible, nests were approached by climbing and examined directly. Since most nests were built at the outer ends of slim upper branches, a pole-mounted mirror was employed to facilitate examination of the contents of the deep nest bowls (see Plate 5.a).

5.1.3 Monitoring breeding progress.

The study area was traversed frequently throughout the springtime, and observations of breeding activity and changes in group size were entered onto nest record cards.

5.1.4 Annual census.

Each January the study area was censused so that all territories were scanned for occupants, and the nonterritorial flock was counted. The results of these counts formed the basis of the productivity analysis.

5.2.0 Results

5.2.1 Clutch Sizes.

In Spring 1979, 8 nests in the study area were examined at least once, allowing 4 clutches to be counted. The mean clutch size was 3.5 (n=4, range 3-4). Two of the nests (one

PLATE 5.a. Pole-mounted mirror used to view magpie nest contents.

containing a partly incubated clutch) were abandoned by the hens in response to repeated human visits. Both females renested, but one of the new nests (containing eggs) was blown out during a storm and the female built a third nest.

Rather than risk further reproductive delays through human interference, it was decided to analyse the sample of clutch sizes collected by the Ornithological Society of New Zealand, through the Society's Nest Records Scheme. Of the 90 cards received for analysis, 73 yielded useful information.

The mean North Island clutch size for white-backed magpies was 3.5 ±1.5 eggs (n=31, range 2-5, 1955-1981), and the mean South Island clutch size was also 3.5 ±1.5 (n=23, range 2-5, 1958-1981). The mean national clutch size was 3.5 ±1.5 eggs. In all samples, the median value was 4.0.

5.2.2 Nestling and Fledgling Survival.

16 of the nest record cards were sufficiently comprehensive for an analysis of nestling mortality. A total of 60 eggs were reduced to 41 nestlings, so that a mortality estimate of 32% was obtained for that stage. Of 17 nestlings counted in 7 nests (4 NI; 3SI), only 9 (53%) fledged, yeilding a mortality estimate of 47% for the fledging transition. Overall, only 15% of the eggs survived to the fledgling stage.

When clutch size was related to nestling number for each of the 16 nests sampled as shown on Table 5.a, it was found that 4-egg clutches comprised 56% of the sample, and that 27 of the 41 nestlings (66%) came from 4-egg clutches.

5.2.3 Reproduction in Pair- and Group-Defended Territories.

In total, 72 nesting events were monitored between Spring 1978 and Summer 1982 (Table 5.b). Of this sample, 46 (64%) events involved hens in group-defended territories, which comprised 70% of the territories in the study area (see section 4.2.4). Productivity was measured as the number of free-flying juveniles (Age Class Three) present in the territory the following January. It was assumed that only one female successfully reproduced during each group-territory breeding event, but the assumption may have been violated in 2 cases. There was no significant variation in productivity from year to year during the study (Kruskal-Wallis $H=5.23$, $n=4$, $P<0.05$).

It was possible to estimate egg-to-fledgling success from knowledge of the average national clutch size, the number of nest attempts in the study area and the final number of juveniles fledged. If an average clutch size of 3.5 eggs is assumed for all nests and all years at Linton, then an estimated 238 eggs gave rise to 90 fledged magpies, 38% of the total possible. There was no difference between pair- and group-defended territories (see Table 5.c), under the assumption that there was only one hen breeding in each of the group-defended territories.

TABLE 5.a

Nestling number counted from clutches of known size

Number of nestlings	Number of eggs				
	2	3	4	5	
1	0	2	0	0	
2	1	1	3	1	
3	0	1	3	1	
4	0	0	3	0	
Total	2	7	27	5	41

Data from OSOC NZ Nest Record Scheme

TABLE 5.b

Production of juveniles by breeding female magpies

	Year			
	1978	1979	1980	1981
n	19	21	20	12
$\bar{x}$	1.6	1.4	0.9	1.4
median	2.0	1.0	1.0	1.5
S	1.0	0.9	0.9	0.6
$S_{\bar{x}}$	0.2	0.2	0.2	0.2
max	4.0	4.0	3.0	2.0
min	0	0	0	0

TABLE 5.c

Fledgling success estimated from
clutch sizes of 3.5

	Pairs	Groups	Total
n	22	46	68
eggs	77	161	238
fledglings	28	62	90
% success	36.0	38.5	38.0

Comparison of production by females in pair- and group-defended territories (Table 5.d) showed that there was no difference in their reproductive performance (P>0.05, Mann-Whitney test).

However, when the same productivity data were analysed on a per capita basis using the Mann-Whitney-Wilcoxon test, paired individuals were found to have a significantly higher productivity than individuals living in groups (P=0.03, Table 5.e).

The results of 46 breeding events in group-defended territories are summarised on Table 5.f. One-half of this sample was from territories defended by trios (two males and one female; one male and two females; one male, one female, one bird of unknown sex), which produced 58% of the juveniles. The remainder were sampled from territories defended by groups of 4, 5 and 6 magpies. Of all the group-territory events sampled, 26% were unsuccessful, 30% led to the production of 1 juvenile and 28% led to the production of 2 juveniles.

A Kruskal-Wallis test of the effect of group size on productivity failed to reject the null hypothesis of no difference.

5.3.0 Discussion

The similarity between the average clutch sizes at Linton and

TABLE 5.d

Female productivity in pair- and group-defended territories

	Pairs	Groups
n	25	47
$\bar{x}$	1.3	1.4
median	1.0	1.0
S	0.7	1.05
$S_{\bar{x}}$	0.1	0.1
max	2.0	4.0
min	0	0

TABLE 5.e

Production *per capita* by adults in pair- and group-defended territories

	Pairs	Groups
n	22	46
$\bar{x}$	0.6	0.4
median	0.5	0.3
S	0.4	0.3
$S_{\bar{x}}$	0.1	0.05
max	1.0	1.3
min	0	0

TABLE 5.f

Number of juvenile magpies fledged in groups of various sizes

Number of Fledglings	Group size 3	4	5	6
0	5	5	1	1
1	6	6	1	1
2	7	4	2	0
3	4	1	1	0
4	1	0	0	0

at Canberra (3.5 eggs, Carrick (1972)), and between the Australian (3.35 eggs, Berggy (1981) unpub.) and New Zealand averages validated comparisons of productivity between the two populations. Although intraspecific latitudinal variations in clutch size are common (Owen 1977), South Island clutches did not differ from the more northern clutches.

Clutch sizes are thought to evolve towards an optimum (measured as the average) determined by clutch size-dependent starvation and clutch size-dependent predation (Ricklefs 1977). Berggy (1981, unpub.) found that 4-egg clutches were the most productive in terms of nestlings raised, and despite the scanty data, this also seemed to be true for the 4-egg clutches sampled by New Zealand ornithologists. This similarity in average and optimal Australian and New Zealand clutch sizes should be investigated along several lines of enquiry. The trait may be accounted for on allometric principles (Western and Ssemakula 1982), may be in the process of changing in the New Zealand population, or may be the outcome of counterbalanced changes in predation and density-dependent food shortages.

The difference in egg-to-fledgling survival between nests visited at intervals by other ornithologists and those monitored from a distance at Linton may reflect the sensitivity to disturbance of incubating magpies. It was found during this study that nests visited during the incubation phase were likely to be abandoned by the hens.

Hens in the Linton study area were 70% more productive than those studied at Canberra (Carrick 1972). Since clutch sizes were not different, the greater productivity at Linton represented better fledging performance. Reasons for improved productivity were discussed in section 2.3.0.

A common theme in studies of cooperatively breeding species has been the question, do helpers help? (Emlen 1978, Verbeek and Butler 1981, Brown et al 1982, Dyer 1983). As Brown (1983) pointed out, helpers must measurably affect the direct fitness of the recipient before indirect (kin) selection can be invoked. (However, if the behaviour is not altruistic the role of indirect fitness cannot be rejected).

Here, reproductive success per breeding effort is used as an index of direct fitness but as Vehrencamp (1979) has argued, only lifetime reproductive success legitimately approximates direct fitness. In the absence of lifetime data from individually identified magpies, the productivity of females sampled at Linton was used perforce as an instantaneous estimate of lifetime reproductive success.

The presence of potential helpers in the territories defended by groups of magpies did not influence the productivity of breeding hens in those territories. Parental care in magpies is unequivocally the responsibility of the functionally monogamous pair within the territory (in the sense of Stacey (1982)), and this explains the lack of difference between the productivity of hens living in pair-defended territories and those in group-defended territories.

Not only did magpie extras have no detectable effect on the reproductive output of breeding pairs, but conditions favouring aid-giving were absent. Charnov (1981) demonstrated that biparental care selects against helpers, even when potentially helping to raise full siblings, until the penalty for leaving home in terms of missed reproductive opportunities drops below 0.5. It was shown in Chapters Two and Three that juvenile dispersal at Linton did not lead to decreased survival. As Koenig and Pitelka (1981) have stated, the reproductive rate of groups on a per capita basis must be higher than that of pairs before the presence of auxiliaries increases the inclusive fitness of helpers or breeders, as long as dispersal and breeding elsewhere is possible. Productivity per capita was significantly lower for group-territory magpies at Linton.

Why did breeders within group-defended territories tolerate the presence of extras, when extra birds did not improve their reproductive success and were not necessarily kin? (Note that the term 'auxiliary' as defined by Dow (1980) cannot be used with respect to magpie group members, since nonbreeding group birds did not help at the nest. The word 'extra' refers to nonbreeding and non-aid-giving group birds which did cooperate in territory defence). So far, the only possible answer to the question is that extra birds were required for their contribution to territorial defence, as described in section 4.3.0. This contribution to the group effort may be thought of as 'birdpower', analogous to terms like manpower and horsepower. In the case of related offspring, retention in the family territory may give rise to the opportunity to bud off a new territory later.

Why did nonbreeders live in territories where they were prevented from breeding? Koenig (1981) suggested that individuals in cooperatively breeding species for which group productivity is no greater than pair output must be "forced" to accept the option of group living in order to obtain access to a localized and limited resource without which reproduction or survivorship are impaired. The evolutionary consequences of each of the four magpie lifestyles can be estimated very crudely by obtaining the product of an animal's *per capita* production, and its coefficient of relatedness to the offspring produced (Vehrencamp 1979). The results of such an exercise for the Linton magpies are shown on Table 5.g. It will be seen that magpies living in pair-defended territories had the greatest estimated average individual fitness and that monogamously-paired adults effectively lowered their fitness by retaining offspring in the territory to form a family group. Although both nomadic flock birds and group-living extras received no genetic benefits, the territorial extras were credited with *per capita* productivity. Group extras appeared to have an opportunity to breed in the future, perhaps by replacing dominant birds of the same sex or

TABLE 5.g

Estimated average individual fitness

Lifestyle	r	R	rR
flock	0	0	0
non-kin group	0	0.33*	0
kin group	0.5	0.33*	0.165
pair	0.5	0.5†	0.250

where r = coefficient of relatedness

and R = *per capita* productivity per breeding effort

* median of 46 samples

† median of 22 samples

overcoming their aggression in exceptionally favourable circumstances. The paradox of cooperation and competition within magpie groups may be viewed as the strategic solution of otherwise nomadic birds to the problem of finding a space to breed. Just what resource shortage fuels the competiton remains unknown.

If reproductive opportunities were so scarce in the Linton population that birds were forced to provide defence assistance in order to become territorial, why did young magpies disperse away from their natal territories? The role of the food supply in the determination of group size is examined in the next chapter.

CHAPTER SIX

Food-Addition Experiment

6.0.0 Introduction

Previously, food has been added to animal territories with the aim of testing hypotheses about territory size, density and reproductive success (Yom-Tov 1974, Källander 1974, Smith et al 1980, Franzblau and Collins 1980, Högstedt 1981, Newton and Marquiss 1981), with variable results. Ewald and Rohwer (1982) extended food supplementation to the study of social systems by successfully inducing polygyny in a population of red-winged blackbirds. In the study reported here, pair-defended magpie territories were supplemented with extra food for 8 months in order to investigate juvenile dispersal behaviour.

Normally, juvenile magpies disperse into the non-territorial flock at the end of their first year, as their female parent begins her next breeding effort (see sections 2.2.2 and 4.2.9). Although the flock lifestyle described by Carrick (1972) for the Canberra magpies led to lower mean monthly weights and reduced survival, the situation at Linton was not as severe (see Chapter Three). However, an estimate of average individual fitness for the flock lifestyle at Linton was 0, compared with 0.165 for family group members and 0.5 for the adults of a monogamous pair. Despite this, and in spite of direct and indirect benefits from aid-giving as an alternative to dispersal described for other species (see 5.1.0, and Emlen 1981), the majority of juvenile magpies dispersed out of their natal territories.

Since the final departure of the yearling birds coincided with the hatching of the next cohort of nestlings, it was hypothesised that a real or socially induced food shortage precipated the transition to a nomadic lifestyle. A prediction arising from this hypothesis was that juvenile dispersal should be delayed or inhibited under conditions of food abundance. Accordingly, extra food was added to a sample of pair-defended territories and the behaviour of the juvenile inhabitants compared with birds living in similar but non-supplemented territories.

6.1.0 Methods

6.1.1 Test and control territories.

In January 1982, 11 territories which were defended by a male-female pair and which contained successfully fledged juveniles (Age Class Three) from the 1981 spring nesting season were identified. Five of these territories were randomly assigned to the Test category, and six became Controls. Altogether there were 7 juveniles in the test territories, and 8 in the controls. In all, 6 of the territories were located outside the study area on other farms at Linton.

6.1.2 Description of food stations.

A single wooden pole was erected in each of the test territories so that its finished height above ground was 2m. Four perches were arranged at right angles near the top, and a 500 ml plastic cup with a perforated base was hung beside each perch. A feeding station is shown in Plate 6.a. Poles were not placed in the control territories.

6.1.3 Description of supplementary food.

From February 1982, chopped defrosted ox heart was delivered daily to each test territory. The diced meat was coated with cooking oil to slow dessication, and a vitamin supplement and calcium powder were sprinkled over the meat when the adults began provisioning the next cohort of nestlings in September. Diced ox heart was found to be highly palatable to hand-reared magpies.

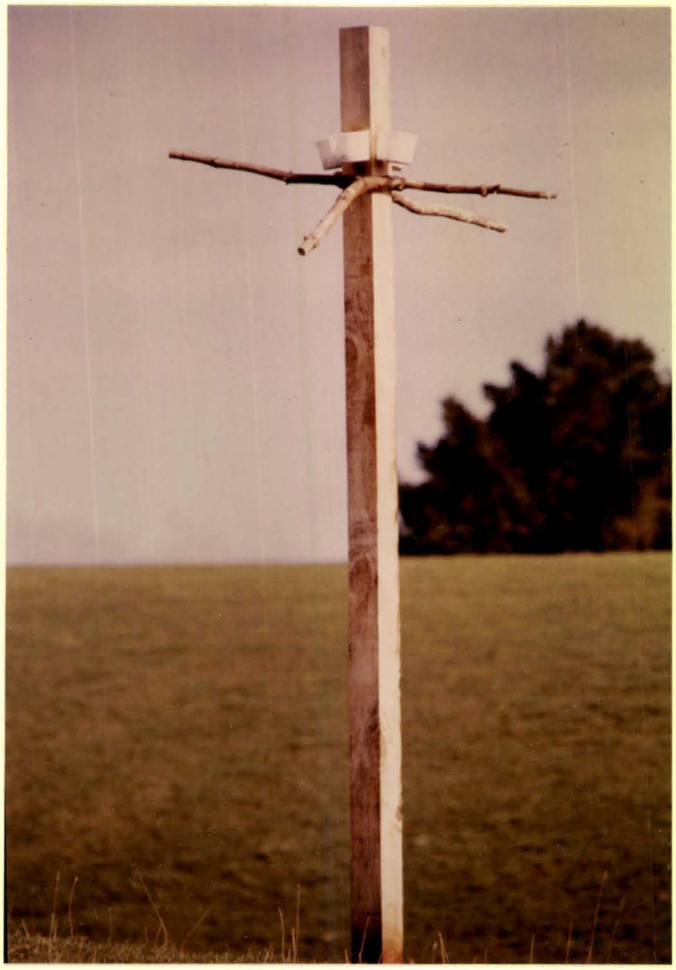
6.1.4 Experimental regime.

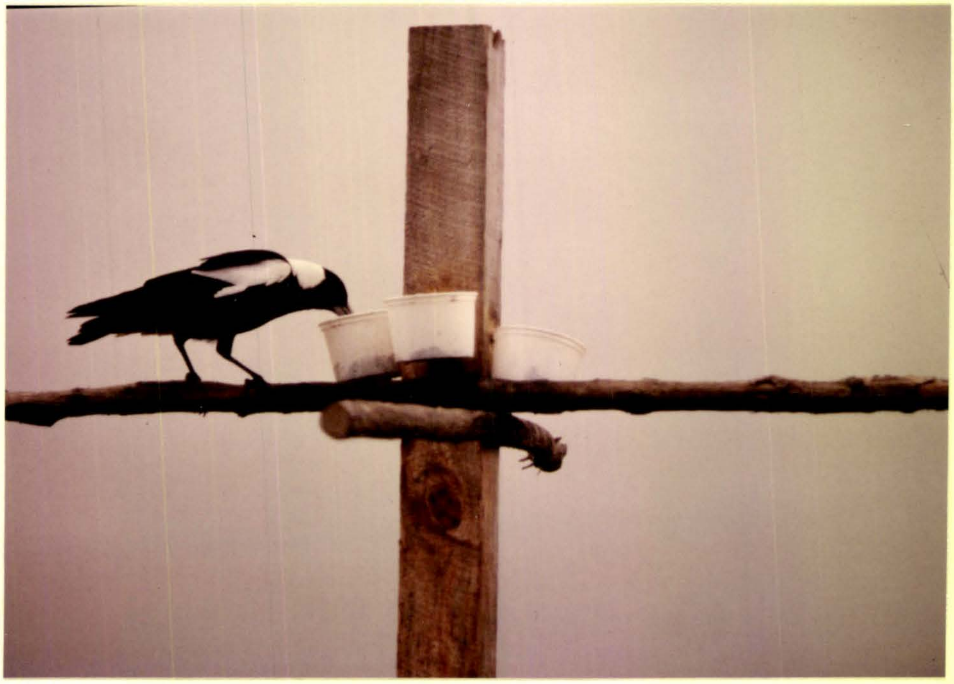
The experiment was initiated in February 1982 when the juveniles fledged in 1981 were independent.

Meat was delivered daily to the test territories in the two hours before dawn, and the amount of meat was adjusted so that

PLATE 6.a. Feeding station.

PLATE 6.b. Male magpie consumes ox-heart at feeding station.





about 15% by weight remained in the cups after 24 hours. The birds were consuming meat within 7 days of its introduction and all magpies in the test territories were checked as using the meat within the first 21 days (see Plate 6.b). No neighbouring magpies and no animals of any other species were ever observed to consume meat from the feeders. One of the control territories abutted onto a test territory.

All territories were regularly checked for the presence of juveniles. Exact dates of juvenile departure were not known, but taken to be the number of days from the beginning of the experiment to the first day an animal was not seen. The length of juvenile stay was therefore slightly overestimated.

Food suplementation was discontinued after 240 days, past the point at which the next juvenile cohort was fledged. The reproductive behaviour of birds in both test and control territories was closely monitored.

6.1.5 Sex of dispersing juveniles.

Age Class Three magpies can not be sexed on visual characters so that the sexes of the 15 birds of that age class in the test and control territories were unknown at the start of the study. Two of these animals were subsequently discovered to be females on behavioural criteria.

6.2.0 Results

6.2.1 Juvenile dispersal.

The 7 juveniles present in the test territories reduced to 3 at the completion of the experiment. Eight control juveniles reduced to 1 yearling (Age Class Four) during the same period. The reduction in numbers was significant for both test and control territories. Supplementary food therefore did not influence the number of juveniles remaining in the territories as extras.

Although most juveniles dispersed from their territories, those living in the territories with an artificial abundance of food may have dispersed later in the year. However, a rank test of medians on the data in Table 6.a could not detect any tendency for magpies in the test territories to remain longer than the control birds.

6.2.2 Polygyny in test territories.

A total of 9 nests were built in the 5 test territories, whereas only 4 were produced in the 6 control territories (see Table 6.b). This was the outcome of nest-building activities by extra females in the formerly pair-defended test territories.

In the 'cowshed' territory (see Table 6.b), the remaining yearling built her own nest, solicited her father and was mated by him at least 4 times. She then sat in the nest for

TABLE 6.a

Length of stay by juvenile magpies (estimated) during food-addition experiment

Test	Control
240	240
130	183
191	115
240	152
145	137
185	137
130	130
Combined median 145	

TABLE 6.b

Number of yearling magpies remaining and nests built in test and control territories at completion of food-addition experiment

Test				Control			
Territory	Juveniles	Yearlings	Nests	Territory	Juveniles	Yearlings	Nests
Cowshed	1	1	2	Silage	1	1	0
a	1	0	2	d	1	0	1
Underwood	2	2	2	Bridge	2	0	0
Mcgovern	2	0	2	Hanlen	2	0	1
Irvine	1	0	1	Cabbage	1	0	1
				Micro.	1	0	1
Total	7	3	9		8	1	4

nearly 5 weeks. No offspring were produced but her mother fledged one chick, after persistently attacking the yearling whenever she solicited.

In territory 'a', an unknown female immigrated into the territory in April, and she also nested without success. The original hen fledged two chicks.

Both juveniles remained in the 'Underwood' territory. One of them built a nest, solicited her father and was mated at least once by him. She also failed to produce young while her female parent fledged two.

Both juveniles in the 'McGovern' territory dispersed, and a unknown adult female joined the territory in July. When her nest failed, she began delivering food to the dominant hen's nestlings. This was the first case of helping by a female ever seen during the study.

No difference in laying dates (determined from the onset of incubation) was detected between test and control territories, and two females in control territories did not even build nests.

6.2.3 Productivity in test and control territories.

A comparison of the productivity of the test and control territories, shown on Table 6.c, could not find any difference

TABLE 6.c

Number of juveniles fledged by female magpies in test and control territories

Test number fledged	Test number females	Test fledged per female	Control number fledged	Control number females	Control fledged per female
1	2	0.5	0	1	0
2	2	1.0	4	1	4.0
2	2	1.0	0	1	0
3	2	1.5	3	1	3.0
2	1	2.0	1	1	1.0
			2	1	2.0
median 2.0	-	1.0	1.5	-	1.5

in the numbers of magpies fledged (Mann-Whitney-Wilcoxon test of medians). Territories receiving extra food did not produce significantly more offspring than the control territories.

There was also no significant difference in the productivity when expressed as the number of juveniles reared per female in the territories (see Table 6.c), although none of the extra females in the test territories raised offspring of their own.

Productivity between years was examined using the Wilcoxon matched-pairs signed ranks test on the data in Table 6.d. The test territories fledged significantly more young in 1982 than in 1981, whereas there was no between-years difference for the control territories. When compared with themselves, test territories were more productive.

6.3.0 Discussion

The hypothesis that juveniles dispersed in response to a shortage of food was rejected, because juveniles dispersed even when food supplies were artificially boosted. The discovery that 2 of the 3 non-dispersing magpies in the test territories were females which attempted to breed (in juvenile plumage), meant that the hypothesis had been framed too simplistically. Instead, the 'decision' to stay or go may have depended on an interaction between the gender of the yearling birds and the food supply in the territory.

TABLE 6.d

Number of juveniles fledged per breeding female in 1981 and 1982, for test and control territories

Test		Control	
1981	1982	1981	1982
1	1	1	0
1	2	1	4
2	2	2	0
2	3	2	3
1	2	1	1
		1	2

Gaston (1978) found that females dispersed away from the natal unit in common babblers, but young males were retained. In two highly social mammalian species, the males dispersed leaving the females to attain reproductive status at home (marmots; Armitage and Johns (1982), hyenas; Owens and Owens (1984)). Differential dispersal has been described for magpies in the Canberra population (Carrick 1972), where yearling males were said to be more likely to disperse than their female counterparts. Unfortunately, there was no description of how this information was obtained. The flock sex ratio at Linton did not appear to be biased in favour of males (see section 2.3.0), so the apparent difference in the fates of yearling males and females was not anticipated..

The induction of polygyny in 4 of the 5 test territories was an unexpected outcome of the altered food regime. Lott (1984) listed 31 species whose mating systems alternated between monogamy and polygyny, two-thirds of which did so in response to altered ecological circumstances ranging from unbalanced sex ratios to changes in resource distribution and abundance. Polygyny may be prevented by a requirement for unshared male parental care (Yasukawa and Searcy 1982), or aggression between females (Emlen 1982, Hannon 1984). However if there are differences in the quality of male territories, females may achieve greater reproductive success by mating with already-mated males in high quality territories than by joining unmated males in lower quality territories (Verner and Willson 1966, Orians 1969).

Since two of the secondary females which attempted to breed in the test territories did so independently rather than assist their parents to raise younger siblings, a payoff in terms of improved individual (rather than inclusive) fitness was sought. Even though none of the secondary females reared offspring of her own, contradictory to the Verner-Willson-Orians model, opportunities for indirect benefits to fitness were not exploited.

Of the 46 group-territory breeding events monitored between 1978 and 1981, 20 (43%) involved territories with more than one adult female. Attempts by subordinate hens to build nests and raise chicks were thwarted by the aggression of the dominant female in each case (see section 4.2.6), and subordinates only rarely succeeded in their efforts. By their aggression, dominant hens maintained an effectively monogamous relationship with their mates, and inhibited the development of polygyny.

It is suggested here that the polygyny observed under the test regime at Linton resulted from a food-induced shift in the polygyny threshold which was detected by the transient and juvenile hens, and a corresponding food-induced reduction of intolerance of primary breeders.

The consequence of group territorial behaviour for males is that as group size increases, the patrimony factor stimulates intragroup competition. The single instance of male helping observed during the study (see section 4.2.8) may have resulted from actual or presumed (in a non-cognitive sense) double-fathering of the clutch being incubated. Only the dominant cock copulated with hens in the territory, and as Gaston (1978) predicted, subordinate males should vacate a group when the decrease in fitness resulting from male-male competition exceeds any increase in fitness through kin selection. Biparental care also selects against the retention of male offspring as helpers (Charnov 1981). Extra males may be recruited into pukeko groups in response to competition from neighbouring groups, by dominant birds caught in a situation analogous to the "prisoners dilemma" (Craig 1984), rather than through indirect fitness effects. It is predicted that dispersal was a mechanism facilitating lifetime reproductive success for young male magpies, by increasing their chances of adopting a more favourable lifestyle. Only longitudinal records from known individuals will confirm or reject the prediction.

In other studies, superabundant food enhanced reproductive performance. For example, chick survival was improved in crows perhaps because adults were able to spend more time at the nest (Yom-Tov 1974), and European magpie pairs (Pica pica) produced more fledglings than control pairs (Högstedt 1981). Additional food led to increased clutch sizes in Sparrowhawks (Newton and Marquiss 1981). During the study reported here, neither production per territory nor production per female differed significantly between test and control territories.

However there was a significant increase in the output of the test territories between 1981 and 1982, while the control territories showed no change. When compared against themselves, the original hens in the test territories were able to fledge more young when the food supply was supplemented, and it was inferred that magpie productivity was at least in part limited by the food supply.

There were two routes to group territoriality in the Linton magpie population; one via retention of offspring in family groups, and the other through group formation in the flock and subsequent efforts to acquire a defended area. Studies of cooperatively breeding species have demonstrated that kin groups form from offspring retention, and aid is given to the primary breeders. Aid-giving by offspring has been variously ascribed to parental suppression of reproduction (Vehrencamp 1979, Emlen 1982) and 'parental facilitation' or tolerance of offspring persistence (Brown and Brown 1984). When magpies were encouraged to retain their yearling offspring, they did not do so (if they had done so, their average individual fitness would have dropped from 0.5 to 0.165). Moreover, birds still in juvenile plumage and immigrants to the test territories attempted to breed. The hypothesis that magpies are cooperative breeders must be rejected. Instead, they must be viewed as selfish opportunists which exploit various social lifestyles in order to obtain a reproductive role.

CHAPTER SEVEN

Discussion and Summary.

7.0.0 Discussion.

7.1.0 Parameters of a magpie population in New Zealand.

There were two reasons for conducting the demographic research reported in Chapters Two, Three and Four of this report.

First, within the adaptationist programme, the study of social systems requires a thorough knowledge of the set of life-history tactics exploited by the individuals within a population. Genetic, physiological, ecological and demographic constraints limit the adaptiveness achieved by organisms in response to environmental (selective) pressures (Mayr 1983). The researcher seeking to discriminate between the effects of chance and of natural selection on patterns of social behaviour therefore needs to discover the generality of observed trends in natality and mortality, and emigration and immigration in the population under study. In practice, this is approximated by setting confidence limits to statistics measured from a sample of the population.

The second reason for collecting demographic data at Linton was to allow comparisons to be drawn with another population in its native environment. If differences in demography and social structures are discovered in the introduced population, then environmental mechanisms of change are inferred.

7.1.1 Population size and density.

The number of territorial magpies remained constant from year to year at Linton, and their density was four times greater than that measured at Canberra (Carrick 1972). Predation was absent at Linton, and the food supply may have been richer. Confirmation from a comparison of prey species levels and capture rates is required.

The density of non-territorial magpies was six times greater in the New Zealand study area, and it is suggested that the habitat occupied by the Australian flock birds was poor in comparison. Whereas insufficient food may have prevented flock birds from attempting to breed at Canberra, some other factor such as the absence of trees and bushes may have inhibited territory establishment on the Linton flock grounds. A simple test of this hypothesis would be the provision of artificial nest sites at the two localities.

7.1.2 Clutch size and productivity.

Despite the evidence for a better food supply at Linton, there were no differences in the average clutch sizes in the two study areas, or between the two countries. The most parsimonious explanation for the similarity is a non-adaptive one: magpie clutch size is linked to body size by allometric principles (Western and Ssemakula 1982). Although an increase in clutch size in richer environments could allow the production of more young, such an adaptive shift may be prevented by 'cohesion of the genotype' (Mayr 1983).

The adaptive explanation was proposed by Lack (1954), who argued that the most productive clutch size will become the most common one through natural selection. In spite of evidence that in many passerines the most productive clutch is larger than the most common one (Klomp 1970), the limitations of food availability and parental effort proposed by Lack still apply (Ricklefs 1977). Four-egg clutches were the most common and successful in Australia (Berggy 1981, unpub.), and were the most common and possibly the most successful in New Zealand. The upper limit on productivity must be set by time constraints on the parents and growth constraints of nestlings, even when the food supply is abundant.

Although clutch sizes were the same in the two populations, breeding females at Linton produced more free-flying young than those at Canberra. Nest losses due to predation could not be measured, but the only potential predator in the district -the harrier hawk- was never seen to rob magpie nests. The absence of predation and the richer food supply evidenced by the high density of magpies at Linton may have combined to improve productivity.

7.1.3 Survival.

The estimated annual survival of territorial magpies at both Linton and Canberra was 0.85. However, the flock estimate was 0.50 at Canberra and 0.90 at Linton. Although this difference in the measured survival of nomadic magpies must be verified, diseased birds were not seen in the Linton flock (in contrast to Canberra), and predation was nil or low. In survival terms, the transition from territoriality to nomadism was not as punitive at Linton.

7.1.4 Operational sex ratios.

The adult sex ratio in the Linton territories was equal, but at Canberra females outnumbered males. The sex ratio in the flock at Linton was difficult to measure but lay between 33:66 and 50:50 males to females, whereas males were numerically superior in the Canberra flock. Either females were preferentially retained in the Canberra terriories, or males were preferentially excluded. One may speculate that in an environment where survival outside territories is low, parents should retain youngsters of the sex with the highest likely reproductive success in order to facilitate their passage to reproductive maturity (Brown and Brown 1984). In the magpie case, females seemed to disperse later than males at Canberra (Carrick 1972).

7.2.0 Four lifestyles in a New Zealand magpie population

Lifestyle was defined in section 4.3.0 as an instantaneous subset of response likelihoods to physical and social stimuli, characterising differences between magpies which are more general than individual differences, but which are not shared by the whole population. In this study four non-overlapping lifestyles were abstracted from the all-occurences sample of social behaviour. Such intra-specific variations in social behaviour have previously been obscured by descriptions of broad species-specific social patterns (Lott 1984), and where magpies were concerned much information about individual variations was lost in a wealth of population-level data (Carrick 1972).

Unfortunately the statistical methodology for distinguishing within-population patterns was too sophisticated for the data collected during this study. On the one hand taxonomists and plant ecologists seek clusters based on similarities or differences between individuals on an array of measured variables (Williams 1971, Mezzich and Solomon 1980), and on the other, a range of multivariate techniques for the reduction of many variable measurements to a few derived variates are available (Maxwell 1977, Aspey and Blankenship 1978). The qualitative criteria used in this study must eventually be superseded by more rigorous procedures.

7.2.1 Nomadism versus territoriality.

Approximately 20% of the magpies in the study area at any time were non-territorial, living in a loosely assembled flock of nomadic individuals. Such flocks formed in the spring from yearling magpies emigrating out of territories, with the addition of some adults displaced from territories.

The territorial spectrum observed at Canberra appeared to be absent at Linton, where most territories were long-term. The abrupt transition between the territorial and flock phases and the longer survival of Linton flock birds indicated that magpie habitat there was more uniform than at Canberra. The less graduated interface between trees and pasture at Linton possibly limited the variety of territory types.

Territory defence levels were highest in the autumn months of March, April and May, at the time when parties of flock birds were flying through and landing in defended areas. From observations of the proportion of flock birds foraging at any time, it seemed that flock birds were experiencing a food shortage in March relative to other months. This reduction in their food supply may have stimulated nomadic magpies to search for food elsewhere, and may have been the proximate cause for the autumn invasions of territories.

The absence of any correlation between territory sizes and the number of magpies living in the territories disproved the hypothesis that magpies were primarily defending a food supply. Other possibilities remain to be investigated, including the idea that in some way, territorial magpies sought to achieve inactive time as an insurance against invasion.

7.2.2 Monogamy versus group-territoriality.

Two of the territorial lifestyles identified during this study involved cooperative defense by groups of magpies. Some of these groups comprised individuals known to be related as parents and subadult offspring. In the others, inter-individual relatedness was unknown but ranged between 0 and 0.5 (siblings).

Pukekos also breed as pairs or groups (Craig 1980), and multi-male groups may form in response to competitive pressure from neighbours (Craig 1984). Some of the groups comprised unrelated pukekos. Such groups were described as having unstable membership, a male-biased sex ratio, promiscuous matings, uncoordinated incubation behaviour, and formed from non-territorial flock birds. From limited observations at Linton and the more extensive Auatralian data (see the case histories in Carrick 1972), non-kin magpie groups formed in the flock and cooperated to obtain a territory. Several seasons may elapse before a breeding attempt succeeds, and groups reduce in size and approach an equal sex ratio during this period. The non-kin group lifestyle seemed to be a stepping stone to monogany and long-term territoriality.

7.3.0 The cooperative breeding hypothesis

Aid-giving to non-descendant relatives is generally termed cooperative breeding (reviewed in Brown 1983), and could have evolved via kin selection or natural selection (Oring 1982). A strong link between group-territorialty and cooperative breeding has been established for many species (Gaston 1978), so it was hypothesized that magpies living in territorial groups at Linton were breeding cooperatively. Indeed, magpies have frequently been cited as cooperative breeders (section 5.0.0).

7.3.1 Strong inference.

A strong inference approach was adopted to test the cooperative breeding hypothesis (Platt 1964). Strong inference results from the systematic application of inductive inference to alternative hypotheses, until all but one (or a few) of them are disproved. If an *a priori* experiment designed to disprove the hypothesis is impossible, one scrutinises the results of an investigation to discover the hypothesis that has been disproved *a postiori*.

In the past, ecological researchers mixed modelling and investigating strategies, and Pielou (1981) has argued that only investigation (equivalent to strong inference) is useful. However, Quinn and Dunham (1983) expressed reservations about the application of strong inference to the analysis of theories of causality in ecology and evolution, on the grounds that single or easily stated null converses are rare. Theirs was a valid complaint, but as shown below, strong inference proved to be invaluable in the analysis of juvenile dispersal behaviour.

7.3.2 Cooperative breeding.

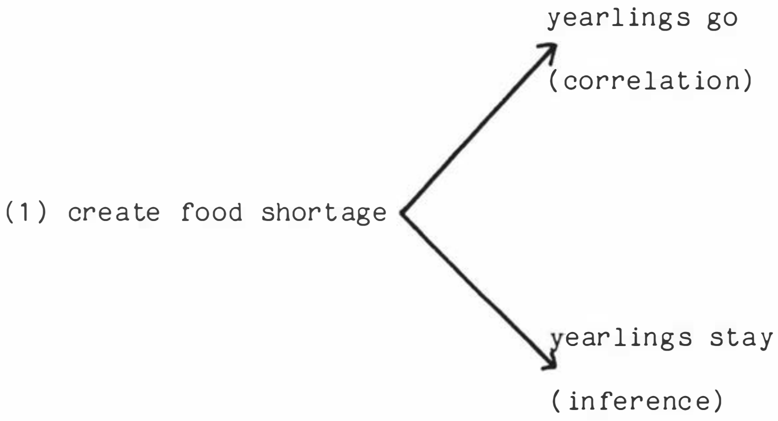
It was theorized that nonbreeding magpies assisted breeders to reproduce, either by providing direct aid during the nesting stage or by indirectly assisting in some other way, such as territory defense. Direct help could be disproved by observation, but the exclusion of indirect help required productivity data. If the group-territory females were more productive than pair-territory females, or if *per capita* production was lower in pair-territories, the hypothesis was disproved.

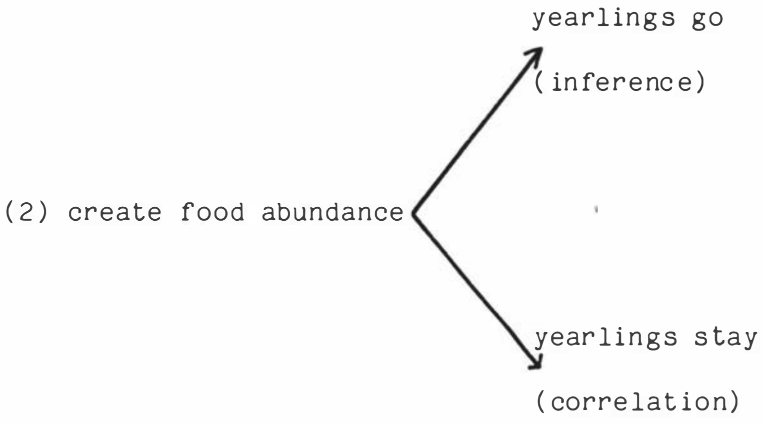
No helping at the nest by nonbreeding offspring was seen at Linton and two instances of adult nest assistance were discounted. No difference in female productivity was discovered, and *per capita* production was lower in the groups. The magpies at Linton did not breed cooperatively.

7.3.3 Delayed juvenile dispersal.

The kin groups that formed in the Linton magpie population resulted from the failure of yearling offspring to disperse. Although delayed maturity and prolonged association of young birds with their parents features in many cooperatively breeding species (Brown 1983), it was not correlated with helping in magpies. Under what conditions do juvenile magpies remain in their natal territories for longer than a year?

It was suggested that juvenile magpies dispersed from their territories because of a food shortage which either forced their parents to reject them, or forced the young birds to feed elsewhere. Two experiments allow this hypothesis to be rejected:





Methods for suppressing earthworm populations on a large scale are available (Tomlin *et al* 1981) but were not compatible with farming operations in the study area. Instead, a food-addition experiment was conducted.

Abundant food neither delayed nor inhibited juvenile departure from territories. The hypothesis that a food shortage stimulated dispersal was rejected by strong inference.

Two additional results were obtained. Pairs receiving extra food became polygynous groups, and the breeding hens in these territories fledged significantly more chicks than they had in the previous year. What hypotheses did these results disprove?

That food supply had no effect on female numbers and breeding behaviour in territories was immediately excluded. In some way, super-abundant food allowed extra females to become established in pair-defended territories. Not only were female offspring permitted to remain and attempt to breed, but other females had somehow detected the enriched food supply and managed to enter the territories. It seemed that the intolerance of the dominant hens described in 4.2.6 had abated under the experimental conditions. Yearling females opted to remain in their natal territories when a breeding attempt was possible.

The hypothesis that food supply does not influence productivity was also rejected. Given the super-abundant food conditions during the experiment, the improvement may have reflected reduced foraging and travelling time constraints on the adults as they provisioned the nestlings.

7.4.0 Summary

Magpies at Linton were not cooperative breeders, based on the evidence accumulated during this study.

Nonterritorial magpies foraged together in flocks, did not have preferred associations with other individuals, and did not breed. The flock sex ratio was probably equal, and a time budget study showed that flock foraging levels were highest in March. Flocks formed in the spring as yearlings emigrated from the territories, and a high survival rate was estimated.

Territorial magpies defended uniformly distributed areas averaging 5 Ha in size, on a permanent basis. One-third of these territories were occupied by pairs, and the remainder by groups of three to eight magpies, with an overall equal sex ratio. Family groups formed when yearlings did not emigrate, and nonkin groups may have formed in the flocks. Group birds spent less time perching and more time defending the territory than pairs. A February food shortage was predicted from the time budgets of the territorial magpies. Clutch sizes averaged 3.5 eggs, and an average annual productivity of 0.96 juveniles per breeding female was recorded. Male parents visited the nestlings as often as the females did, and production was enhanced by super-abundant food.

Nonbreeding birds did not help at the nest, except on rare occasions. Females living in group-defended territories did not rear more offspring than those in pairs, and *per capita* production was lower for group magpies.

When the food supply was supplemented in a sample of pair-defended territories, juveniles did not remain to form family groups. Instead, twice as many nests were built as the result of the activities of subordinate females who remained in or entered the supplemented territories, and attempted to breed.

Non-kin-group territoriality in magpies may have operated as a stepping stone between nomadism and permanent reproductive status, while kin-group territoriality may have sometimes facilitated juvenile transition to permanent reproductive status.

APPENDIX

TABLE ONE

Number of visits and sights in 12 closely-watched magpie territories, and number of sightings needed for 90% census efficiency (when visit efficiency of 60% is set)

Territory	Year											
	1979			1980			1981			1982		
	V	R_A	R_T	V	R_A	R_T	V	R_A	R_T	V	R_A	R_T
[01]	11	54	5	3	7	2	1	3	2	3	10	2
[02]	7	16	3	6	24	2	4	10	2	5	17	2
[03]	7	24	3	6	18	2	4	14	2	12	33	5
[04]	8	29	3	8	18	3	5	10	2	14	39	7
[05]	7	13	3	5	18	2	2	6	2	3	9	2
[06]	13	32	7	5	13	2	0	0	2	5	12	2
[10]	7	14	3	5	8	2	2	3	2	1	3	2
[11]	6	18	2	5	15	2	2	5	2	3	9	2
[12]	3	15	2	8	39	3	3	7	2	3	8	2
[16]	3	5	2	2	4	2	2	4	2	2	6	2
[17]	8	28	3	9	39	4	3	9	2	3	11	2
[21]	7	42	3	4	22	2	3	13	2	1	5	2

R_A = actual number of sightings

R_T = number of sightings required for 90% census efficiency (from Svennson (1978))

APPENDIX

☐ TIMES PAIR SIGHTED

⬡ TIMES INDIVIDUAL SIGHTED

	RYG	RGR	RGW	RGB	RGY	WRW	WRB	WRY	WRG	WBR	WBW	WBY	WBG	WYR	WYW	WRB	WYG	WGR	WGW	WGB	WGY	BRW	BRB	BRY	BRG
RYG	0																								
RGR		1																							
RGW		1	1																						
RGB				0																					
RGY					1																				
WRW						0																			
WRB							0																		
WRY		1	1					1																	
WRG									0																
WBR		1	1					1		1															
WBW		1	1					1		1	1														
WBY		1	1					1		1	1	1													
WBG		1	1					1	1	1	1	1	2												
WYR		1	1					1	1	1	1	1	2	4											
WYW					1										1										
WRB																0									
WYG		1	1					1	1	1	1	1	2	2			2								
WGR																		0							
WGW																			0						
WGB					1										1					1					
WGY														1							1				
BRW					1										1					1		1			
BRB																							0		
BRY		1	1		1				2	1	1	1	2	3	1		2			1		1		6	
BRG		1	1					1		1	1	1	1	1			1							1	1

FIGURE 1. Sightings of individually banded flock magpies from October 1978 to April 1979.

REFERENCES

Altmann, J. (1974) Observational study of behavior: Sampling methods. Behaviour 48: 227-267.

Armitage, K.B. (1982). Social dynamics of juvenile marmots: role of kinship and individual variability. Behav. Ecol. Sociobiol. 11: 33-36.

Armitage, K.B.; Johns, D.W. (1982). Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. Behav. Ecol. Sociobiol. 11: 55-63.

Arnold, G.W.; Grassia, A. (1983). Social interactions amongst beef cows when competing for food. Appl. Anim. Ethol. 9: 239-252.

Aspey, W.P.; Blankenship, J.E. (1978). Comparative ethometrics: congruence of different multivariate analyses applied to the same ethological data. Behav. Processes 3: 173-195.

Atwood, J.L. (1980). Social interactions in the Santa Cruz Island scrub jay. Condor 82: 440-448.

Balda, R.P. (1981). Sociobiology as learned from a drab, blue bird. Auk 98: 415-417.

Barnard, C.J. (1980). Flock feeding and time budgets in the house sparrow (Passer domesticus L.). Anim. Behav. 28: 295-309.

Begon, M. (1979). Investigating Animal Abundance. London. Edward Arnold.

Bekoff, M.; Wells, M.C. (1982). Behavioural ecology of coyotes: social organization, rearing patterns, space use and resource defense. Zeitschr. Tierpsychol. 60: 281-305.

Berggy, J. (1981). Analysis of nest records of the black-backed magpie. Unpublished student project.

University of New England, Armidale.

Best, L.B. (1975). Interpretational errors in the "mapping method" as a census technique. Auk 92:452-460.

Biedenweg, D.W. (1983). Time and energy budgets of the mocking bird (*Mimus polyglottos*) during the breeding season. Auk 100: 149-160.

Brown, J.L. (1964). The evolution of diversity in avian territorial systems. Wilson Bulletin 76: 160-169.

Brown, J.L. (1974). Alternative routes to sociality in jays - with a theory for the evolution of altruism and communal breeding. Amer. Zool. 14: 63-80.

Brown, J.L. (1983). Cooperation - a biologist's dilemma. Adv. Study Behav. 13: 1-37.

Brown. J.L.; Brown, E.R. (1981). Kin selection and individual selection in babblers. In Alexander, R.D.; Tinkle, D.W. (eds). Natural Selection and Social Behaviour. New York. Chiron.

Brown, J.L.; Brown, E.R. (1984). Parental facilitation: parent-offspring relations in communally breeding birds. Behav. Ecol. Sociobiol. 14: 203-209.

Brown, J.L.; Brown, E.R.; Brown, S.D.; Dow, D.D. (1982). Helpers: effects of experimental removal on reproductive success. Science 215: 421-422.

Brown, J.L.; Orians, G,H. (1970). Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1: 239-262

Bull, P.C.; Gaze, P.D.; Robertson, C.J.R. (1978). Bird Distribution in New Zealand Wellington. Ornithological Society of New Zealand.

Burger, J. (1981). Super territories: a comment. Amer. Nat. 118: 578-580.

Caraco, T. (1979a). Time budgeting and group size: a theory. Ecology 60: 611-617.

Caraco, T. (1979b). Time budgeting and group size: a test of theory. Ecology 60: 618-627.

Carrick, R. (1963). Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. Proc. 13th. Int. Ornithol. Congr. :740-753.

Carrick, R. (1972). Population ecology of the Australian black-backed magpie, royal penguin and silver gull. Wildl. Res. Rep. U.S. Dept. Interior No. 2.

Charnov, E.L. (1981). Kin selection and helpers at the nest: effects of paternity and biparental care. Anim. Behav. 29: 631-632.

Clarke, M.F. (1984). Co-operative breeding by the Australian Bell Miner *Manorina melanophrys* Latham: A test of kin selection theory. Behav. Ecol. Sociobiol. 14: 137-146.

Clark, P.J.; Evans,F.C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

Clark, C.W.; Mangel, M. (1984). Foraging and flocking strategies: information in an uncertain environment. Amer. Nat. 123: 626-641.

Cole, C.F. (1921). Variations in the black-backed magpie (*Gymnorhina tibicen*). Emu 21: 51-54.

Colgan, P. (1979). Is a super-territory strategy stable? Amer. Nat. 114: 604-605.

Colmenares, R. (1983). Structure sociale d'une bande de loups iberiques (*Canis lupus signatus*) en captivite. Biol. Behav. 8: 27-47.

Craig, J.L. (1980). Pair and group breeding behaviour of a communal gallinule, the pukeko, *Porphyrio p.*

melanotus. Anim. Behav. 28: 593-603.

Craig, J.L. (1984). Are communal pukeko caught in the prisoner's dilemma? Behav. Ecol. Sociobiol. 14: 147-150.

Crook, J.H. (1965). The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14: 181-218.

Davies, N.B. (1978). Ecological questions about territorial behaviour. In Krebs, J.R.; Davies, N.B. (eds). Behavioural Ecology. Oxford. Blackwell.

Davis, D.E. (ed.) (1982). CRC Handbook of Census Methods for Terrestrial Vertebrates. Florida. CRC Press Inc.

Dawkins, R. (1976). The Selfish Gene. Oxford. Oxford University Press.

Dow, D.D. (1980). Communally breeding Australian birds with an analysis of distributional and environmental factors. Emu 80: 121-140.

Dunbar, R.I.M. (1982). Adaptation, fitness and the evolutionary tautology. In King's College Sociobiology Group (ed). Current Problems in Sociobiology. Cambridge. Cambridge University Press.

Dunbar, R.I.M. (1983). Life history tactics and alternative strategies of reproduction. In Bateson, P. (ed). Mate Choice. Cambridge. Cambridge University Press.

Duncan, P. (1980). Time-budgets of Camargue horses. II. Time-budgets of adult horses and weaned sub-adults. Behav. 72: 26-49.

Dyer, M. (1983). Effect of nest helpers on growth of redthroated bee-eaters. Ostrich 54: 43-46.

Ekman, J. (1979). Coherence, composition and territories of winter social groups of the Willow Tit Parus montanus and the Crested Tit P. cristatus. Ornis Scand. 10: 56-68.

Emlen, S.T. (1978). Cooperative breeding. In Krebs, J.R.; Davies, N.B. (eds). Behavioural Ecology. Oxford. Blackwell.

Emlen, S.T. (1981). The ornithological roots of sociobiology. Auk 98: 400-403.

Emlen, S.T. (1981). Altruism, kinship and reciprocity in the white-fronted bee-eater. In Alexander, R.D.; Tinkle, D.W. (eds). Natural Selection and Social Behaviour. New York. Chiron.

Emlen, S.T. (1982). The evolution of helping. II. The role of behavioral conflict. Amer. Nat. 119: 40-53.

Ettinger, A.O.; King, J.R. (1980). Time and energy budgets of the willow flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533-546.

Ewald, P.W.; Rohwer, S. (1982). Effects of supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds Agelaius phoeniceus. J. Anim. Ecol. 51: 429-450.

Ficken, M.S.; Witkin, S.R.; Weise, C.M. (1981). Associations among members of a Black-capped Chickadee flock. Behav. Ecol. Sociobiol. 8: 245-249

Fisher, R.A.; Ford, E.B. (1947). The spread of a gene in natural conditions in a colony of the moth Panaxia dominula L. Heredity 1: 143-174.

Fitzpatrick, J.W.; Woolfenden, G.E. (1981). Demography is a cornerstone of sociobiology. Auk 98: 406-407.

Franzblau, M.A.; Collins, J.P. (1980). Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing prey abundance. Oecologia 46: 164-170.

Gartlan, J.S. (1968). Structure and function in a primate society. Folia Primatol. 8: 89-120.

Gaston, A.J. (1978). Ecology of the common babbler Turdoides caudatus. Ibis 120: 415-432.

Gaston, A.J. (1978). The evolution of group territorial behavior and cooperative breeding. Amer. Nat. 112: 1091-1100.

Getty, T. (1979). On the benefits of aggression: the adaptiveness of inhibition and super territories. Amer. Nat. 114: 605-609.

Gould, S.J.; Lewontin, R.C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. Lond. B. 205: 581-598.

Grimes, L.G. (1980). Observations of group behaviour and breeding biology of the yellow-billed shrike Corvinella corvina. Ibis 122: 166-192.

Hamilton, W.D. (1963). The evolution of altruistic behavior. Amer. Nat. 97: 354-356.

Hannon, S. J. (1984). Factors limiting polygyny in the willow ptarmigan. Anim. Behav. 32: 153-161.

Harrigan, K.E.; Arundel, J.H. (1978). Syngamus trachea infections in the white-backed magpie (Gymnorhina hypoleuca). Aust. Vet. J. 54: 360-361.

Harrigan, K.E.; Barker, I.K.; Studdert, M.J. (1975). Poxvirus infection in the white-backed magpie (Gymnorhina hypoleuca) and pox-like conditions in other birds in Australia. J. Wildl. Diseases 11: 343-347.

Herbers, J.M. (1981). Time resources and laziness in animals. Oecologia 49: 252-262.

Hinde, R.A. (1981). Animal signals: ethological and games theory approaches are not incompatible. Anim. Behav. 29: 535-542.

Högstedt, G. (1981). Effect of additional food on reproductive success in the magpie (Pica pica). J. Anim. Ecol. 50: 219-229.

Hughes, J.M. (1982). An explanation for the asymmetrical 'hybrid' zone between white-backed and black-backed magpies. Emu 82: 50-53.

Hughes, J.M.; Pearce, B.J.; Vockenson, K. (1983). Territories of the Australian magpie Gymnorhina tibicen in southeast Queensland. Emu 83: 108-111.

Joste, N.E.; Koenig, W.D.; Mumme, R.L.; Pitelka, F.A. (1982). Intragroup dynamics of a cooperative breeder: an analysis of reproductive roles in the acorn woodpecker. Behav. Ecol. Sociobiol. 11: 195-201.

Källander, H. (1974). Advancement of laying of great tits by the provision of food. Ibis 116: 365-367.

Kiley-Worthington, M. (1978). The social organization of a small captive group of eland, oryx and roan antelope with an analysis of personality profiles. Behav. 66: 32-55.

Kleinbaum,D.G.; Kupper,L.L. (1978). Applied Regression Analysis and Other Multivariable Methods. California. Duxbury Press.

Klomp, H. (1970). The determination of clutch size in birds. A review. Ardea 58: 1-124.

Koenig, W.D. (1981). Reproductive success, group size and the evolution of cooperative breeding in the acorn woodpecker. Amer. Nat. 117: 421-443.

Koenig, W.D.; Pitelka, F.A. (1981). Ecological factors and kin selection in the evolution of cooperative breeding in birds. In Alexander, R.D.; Tinkle, D.W. (eds). Natural Selection and Social Behaviour. New York. Chiron.

Krebs, J.R. (1971). Territory and breeding density in the great tit *Parus major* L. Ecology 52: 2-22.

Lack, D. (1954). The natural regulation of animal numbers. Oxford. Clarendon Press.

Lehner, P.N. (1979). Handbook of Ethological Methods. New York. Garland STPM.

Ligon, J.D. (1981). Demographic patterns and communal breeding in the green woodhoopoe (*Phoeniculus purpureus*). In Alexander, R.D.; Tinkle, D.W. (eds). Natural Selection and Social Behaviour. New York. Chiron.

Ligon, J.D. (1983). Cooperation and reciprocity in avian social systems. Amer. Nat. 121: 366-384.

Ligon, J.D.; Ligon, S.H. (1983). Reciprocity in the green woodhoopoe (*Phoeniculus purpureus*). Anim. Behav. 31: 480-489.

Lott, D.F. (1984). Intraspecific variation in the social systems of wild vertebrates. Behav. 88: 266-325.

Martin, P. (1982). The energy cost of play: definition and estimation. Anim. Behav. 30: 294-295.

Maxwell, A.E. (1977). Multivariate analysis in Behavioural Research. London. Chapman and Hall.

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. J. Theor. Biol. 47: 209-221.

Mayr, E. (1983). How to carry out the adaptationist program? Amer. Nat. 121: 324-334.

McCaskill, L.W. (1945). Preliminary report on the present position of the Australian magpies (Gymnorhina hypoleuca and Gymnorhina tibicen) in New Zealand. N.Z. Bird Notes 1: 86-104.

McIlroy, J.C. (1968). The biology of magpies (Gymnorhina spp.) in New Zealand. Unpublished M.Ag.Sc. Thesis Lincoln College.

Mezzich, J.E.; Solomon, H. (1980). Taxonomy and Behavioral Science London. Academic.

Michod, R.E. (1982). The theory of kin selection. Ann. Rev. Ecol. Syst. 13: 23-55

Mills, M.G.L. (1982). Factors affecting group size and territory size of the brown hyaena, Hyaena brunnea in the Southern Kalahari. J. Zool., Lond. 198: 39-51.

Mumme, R.L.; Koenig, W.D.; Pitelka, F.A. (1983). Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. Nature 306: 583-584.

Myers, J.P. (1983). Space, time and the patterns of individual associations in a group-living species: sanderlings have no friends. Behav. Ecol. Sociobiol. 12: 129-134.

Newton, I.; Marquiss, M. (1981). Effect of additional food on laying dates and clutch sizes of sparrowhawks. Ornis Scand. 12: 224-229.

Nie, N.H.; Hull, C.H.; Jenkins, J.G.; Steinbrenner, K.; Bent. D. (1975). Statistical Package for the Social Sciences. New York. McGraw-Hill.

Orians, G.H. (1961). The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

Orians, G.H. (1969). On the evolution of mating systems in birds and mammals. Amer. Nat. 103: 589-603.

Oring, L.W. (1982). Avian mating systems. In Farner, D.S.; King, J.R.; Parkes, K.C. (eds). Avian Biology vol VI. New York. Academic.

Ornithological Society of New Zealand Inc. The Checklist Committee. (1970). Annotated Checklist of the Birds of New Zealand Wellington. Reed.

Owen, D.F. (1977). Latitudinal gradients in clutch size: an extension of David Lack's theory. In Stonehouse, B.; Perrins, C. (eds). Evolutionary Ecology. London. MacMillan.

Owens, D.D.; Owens, M.J. (1984). Helping behaviour in brown hyenas. Nature 308: 843-845.

Parker, G.A.; Knowlton, N. (1980). The evolution of territory size - some ESS models. J. Theor. Biol. 84: 445-476.

Parkes, K.C. (1982). Subspecific taxonomy: unfashionable does not mean irrelevant. Auk 99: 596-598.

Pellis, S.M. (1981). Exploration and play in the behavioural development of the Australian magpie Gymnorhina tibicen. Bird Behav. 3: 37-49.

Pellis, S.M. (1981). A description of social play by the Australian magpie Gymnorhina tibicen based on Eshkol-Wachman notation. Bird Behav. 3: 61-79.

Phillips, A.R. (1982). Subspecies and species: fundamentals, needs and obstacles. Auk 99: 612-615.

Pielou, E.C. (1981). The usefulness of ecological models: a stock-taking. Quart. Rev. Biol. 56: 17-31.

Pizzey, G. (1980, 1983). A Field Guide to the Birds of Australia. Sydney. Collins.

Platt, J.R. (1964). Strong inference. Science 146: 347-353.

Price, T.; Millington, S.; Grant, P. (1983). Helping in the nest in Darwin's finches as misdirected parental care. Auk 100: 192-194.

Pyke, G.H. (1979). The economics of territory size and time budget in the golden-winged sunbird. Amer. Nat. 114: 131-145.

Quinn, J.F.; Dunham, A.E. (1983). On hypothesis testing in ecology and evolution. Amer. Nat. 122: 602-617.

Reed, E.S. (1981). The lawfulness of natural selection. Amer. Nat. 118: 61-71.

Ricklefs, R.E. (1975). The evolution of cooperative breeding in birds. Ibis 117: 531-534.

Ricklefs, R.E. (1977). A note on the evolution of clutch size in altricial birds. In Stonehouse, B.; Perrins, C. (eds). Evolutionary Ecology London. MacMillan.

Robinson, A. (1956). The annual reproductory cycle of the magpie, Gymnorhina dorsalis Campbell, in south-western Australia. Emu 56(4): 233-336.

Rodman, P.S. (1981). Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. Amer.Nat 118: 275-283.

Rollo, C.D.; Vertinsky, I.B.; Wellington, W.G.; Kanetkar, V.K. (1983). Alternative risk-taking styles: the case of time-budgeting strategies of terrestrial gastropods. Res. Popul. Ecol. 25: 321-335.

Rothamsted Experimental Station (1980). Genstat. Oxford. Numerical Algorithms Group.

Rowley, I. (1976). Co-operative breeding in Australian birds. Proc. 16th. Int. Ornithol. Congr. : 657-666.

Rowley, I. (1981). The communal way of life in the splendid wren, *Malurus splendens*. *Zeitschr. Tierpsychol.* 55: 228-267.

Ryan, T.A.; Joiner, B.L.; Ryan, B.F. (1976). *Minitab*. Massachusetts. Duxbury Press.

Schodde, R. (1975). *Interim List of Australian Songbirds*. Melbourne. Royal Australian Ornithologists Union.

Schoener, T.W. (1968). Sizes of feeding territories among birds. *Ecology* 49: 123-141.

Schoener, T.W. (1983). Simple models of optimal feeding-territory size: a reconciliation. *Amer.Nat.* 121: 608-629.

Schulman, S.R.; Rubenstein, D.I. (1983). Kinship, need and the distribution of altruism. *Amer. Nat.* 121: 776-788.

Serventy, D.L. (1969). *An Index of Australian Bird Names*. Canberra. Commonwealth Scientific and Industrial Research Organization.

Shurcliffe, A.; Shurcliffe, K. (1974). Territory in the Australian magpie (*Gymnorhina tibicen*): an analysis of its size and change. *South. Aust. Ornithol.* 26: 127-132.

Sicker, H.L. (1946). Mating display in the magpie. *Emu* 46: 75-76.

Smith, S. (1978). The "underworld" in a territorial sparrow: adaptive strategy for floaters. *Amer. Nat.* 112: 571-582.

Smith, J.N.M.; Montgomerie, R.D.; Taitt, M.J.; Yom-Tov, Y. (1980). A winter feeding experiment on an island Song Sparrow population. *Oecologia* 47: 164-170.

Stacey, P.B. (1982). Female promiscuity and male reproductive success in social birds and mammals. *Amer. Nat.* 120: 51-64.

Stallcup, J.A.; Woolfenden, G.E. (1978). Family status and contributions to breeding by Florida scrub jays. Anim. Behav. 26: 1144-1156.

Steel, R.G.D.; Torrie, J.H. (1960). Principles and Procedures of Statistics. New York. McGraw-Hill.

Svensson, S.E. (1978). Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. J. Appl. Ecol. 16: 61-68.

Taylor, L.R.; Woiwood, I.P.; Perry, J.N. (1978). The density-dependence of spatial behaviour and the rarity of randomness. J. An. Ecol. 47: 383-406.

Thomson, G.M. (1922). The Naturalisation of Animals and Plants in New Zealand. Cambridge. Cambridge University Press.

Thompson, W.A.; Vertinsky, I.; Krebs, J.R.; (1974). The survival value of flocking in birds: a simulation model. J. Anim. Ecol. 43: 785-808.

Tomlin, A.D.; Tolman, J.H.; Thorn, G.D. (1981). Suppression of earthworm (Lumbricus terrestris) populations around an airport by soil applications of the fungicide, benomyl. Protection Ecology 2: 319-324.

Turner, D.C. (1979). An analysis of time-budgeting by roe deer (Capreolus capreolus) in an agricultural area. Behav. 71: 246-292.

van der Steen, W.J. (1983). Methodological problems in evolutionary biology. I. Testability and tautologies. Acta Boitheoretica 32: 207-215.

Vehrencamp, S.L. (1979). The roles of individual, kin and group selection in the evolution of sociality. In Marler, P.; Vandenbergh, J.G. (eds). Handbook of Behavioral Neurobiology. vol 3. Social Behaviour and Communication.

Verbeek, N.A.M. (1972). Daily and annual time budget of the yellow-billed magpie. Auk 89: 567-582.

Verbeek, N.A.M.; Butler, R.W. (1981). Cooperative breeding of the Northwestern crow Corvus caurinus in British Columbia. Ibis 123: 183-189.

Verner, J. (1965). Time budget of the male long-billed marsh wren during the breeding season. Condor 67: 125-139

Verner, J. (1977). On the adaptive significance of territoriality Amer. Nat. 111: 769-775.

Verner, J.; Willson, M.F. (1966). The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143-147

Vestjens, W.J.M.; Carrick, R. (1974). Food of the black-backed magpie Gymnorhina t. tibicen at Canberra. Aust. Wildl. Res. 1: 71-83.

von Schantz, T. (1984a). Spacing strategies, kin selection and population regulation in altricial vertebrates. Oikos 42: 48-58.

von Schantz, T. (1984b). 'Non-breeders' in the red fox Vulpes vulpes: a case of resource surplus. Oikos 42: 59-65.

Waser, P.M. (1981). Sociality or territorial defense? The influence of resource renewal. Behav. Ecol. Sociobiol. 8: 231-237.

Wasserman, F.E. (1982). The spatial distribution of singing and foraging in the territories of white-throated sparrows. Can. J. Zool. 60: 2757-2760.

Weigel, R.M. (1981). The distribution of altruism among kin: a mathematical model. Amer. Nat. 118: 191-201.

West Eberhard, M.J. (1975). The evolution of social behaviour by kin selection. Quart. Rev. Biol. 50: 1-33.

Western, D.; Ssemakula, J. (1982). Life history patterns in birds and mammals and their evolutionary interpretation. Oecologia 54: 281-290.

Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. Nature 308: 181-184.

Williams, W.T. (1971). Principles of clustering. Ann. Rev. Ecol. Syst. 2: 303-326.

Wolf, L.L.; Hainsworth, F.R. (1971). Time and energy budgets of territorial hummingbirds. Ecology 52: 980-988.

Woolfenden, G.E.; Fitzpatrick, J.W. (1978). The inheritance of territory in group-breeding birds. Bioscience 28: 104-108.

Wynne-Edwards, V.C. (1962). Animal Dispersion in Relation to Social Behaviour. Edinburgh. Oliver and Boyd.

Yasukawa, K.; Searcy, W.A. (1982). Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11: 13-17.

Yom-Tov, Y. (1974). The effect of food and predation on breeding density and success, clutch size and laying date of the crow (Corvus corone L.). J. Anim. Ecol. 43: 479-498.

Zahavi, A. (1976). Co-operative nesting in eurasian birds. Proc. 16th. Int. Ornithol. Congr. : 685-693.

Zar, J.H. (1974). Biostastical Analysis. New Jersey. Prentice-Hall.

Zusi, R.L. (1982). Intraspecific variation and the subspecies concept. Auk 99: 606-608.